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# Apomixis in Systematics, Evolution and Phylogenetics of Angiosperms: Current Developments and Prospects

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## ABSTRACT

Apomixis, the reproduction via asexually formed seed, is taxonomically scattered in angiosperms. Here we review the major developmental pathways to apomixis and the occurrences on the level of orders and families. We provide surveys of large families for which occurrences and evolutionary pathways of apomixis are well documented (Poaceae, Ranunculaceae, Plumbaginaceae, Rosaceae, Brassicaceae, Rutaceae, and Asteraceae). Molecular phylogenetic, phylogenomic, and cytogenetic studies have confirmed that apomixis frequently arises in hybrids, with or without polyploidy. Multiple origins, different developmental pathways, and genetic/epigenetic control mechanisms confirm that apomixis is a derived trait. Pollen functions are in many taxa maintained for fertilization of polar nuclei and proper endosperm development, which allows also for maintenance of facultative sexuality and further intercrossing of lineages. This way, apomixis often results in huge and dynamic complexes of numerous hybrid genotypes and phenotypes with highly reticulate relationships. Such complexes are successful to establish in various habitats and geographical regions. Expression of apomixis appears to be in some genera influenced by environmental conditions. The diversity of evolutionary pathways is reflected in various, genus-wise taxonomic treatments. Future research is needed to understand the short-term evolutionary dynamics, the functional background for apomixis, and the long-term evolutionary fates of apomictic lineages.



## KEYWORDS


agamospermy; embryology; reticulate evolution; phylogenetics; polyploidy; systematics

## I. Introduction

Apomixis, the form of reproduction via asexually formed seeds (Asker and Jerling, 1992), is long known in angiosperms. Already, Gregor Mendel was confronted with unusual inheritance patterns in his crossing experiments of sexual and apomictic hawkweeds (genus *Hieracium* s.l.), but only after the discovery of parthenogenesis by Juel in 1898 the modes of asexual inheritance became understandable (Nogler, 2006). Apomixis attracted early attention of

developmental biologists, geneticists, and evolutionary biologists. Ernst (1918) summarized the major developmental pathways and recognized that apomixis frequently results from interspecific hybridization. Gustafsson (1946; 1947a; 1947b), Asker and Jerling (1992), Naumova (1993) and Carman (1997) outlined the major developmental pathways: gametophytic apomixis involves the formation of an unreduced embryo sac, either via apospory (from a somatic nucellus cell) or via diplospory (from a restitutional

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meiosis or mitoses of the megaspore mother cell); the unreduced egg cell develops without fertilization via parthenogenesis. Sporophytic apomixis initiates the development of an embryo out of somatic cell of ovule, either from the nucellus or the integuments. These embryos often form additionally to sexual embryos, and therefore this pathway is called adventitious embryony. Both gametophytic and sporophytic apomixis results in clonal offspring, but often remains facultative, i.e. in the same generation the plant forms seeds via the normal sexual pathway (with meiosis and fertilization of reduced egg cells) and apomictic seeds. Moreover, gametophytic apomixis can be partial (term after Hojsgaard and Hörandl, 2019), either with unreduced embryo sac formation combined with fertilization of the egg cell (forming so-called B<sub>III</sub> hybrids) or via haploid parthenogenesis (apomeiosis without fertilization). These two pathways occur in progenies and in natural populations of apomictic taxa usually at very low frequencies (Bicknell *et al.*, 2003; Schinkel *et al.*, 2017), but they may also appear rarely in otherwise obligate sexual taxa (Asker and Jerling, 1992).

The evolution of apomictic taxa attracted early attention in systematics research. The evolution of huge and diverse agamic polyploid complexes from hybrids of the sexual progenitor species was recognized in the example of *Crepis* (Babcock and Stebbins, 1938). Multiple origins of hybrids, Mendelian segregation in the first (sexual) hybrid generations, and occasional crossings between facultative apomictic lineages have often resulted in a huge diversity of lineages with distinct morphotypes, cytotypes, and ecotypes (Barke *et al.*, 2018; Hojsgaard and Hörandl, 2019). These lineages might be fixed by apomixis as numerous slightly distinct clones. This evolutionary pathway to diverse apomictic polyploid complexes was described by Grant (1981) for many genera and confirmed in numerous molecular case studies (reviewed by Hojsgaard and Hörandl, 2019). Quite often, more than two progenitor species are involved in hybrid origins, thereby increasing genetic and morphological complexity (e.g. Mráz *et al.*, 2019; Karbstein *et al.*, 2022). Such apomictic polyploid complexes do mostly occur in taxa with gametophytic apomixis and in allopolyploids, whereas autopolyploids usually do not diversify into many different lineages (Hörandl, 2018). In contrast, the association of polyploidy and hybridization to sporophytic apomixis is less obvious, although some genera do show a high complexity of interspecific relationships, e.g. in *Citrus* (Curk *et al.*, 2016). Nevertheless, in many species adventitious embryony appears just as a reproductive feature of traditionally classified species.

The reticulate evolution of such agamic complexes does not fit to traditional phylogenetic concepts of bifurcating phylogenies, and therefore also the recognition of relationships of lineages is still a methodical challenge, even in the era of genomics. Quite often, morphological and genetic data are incongruent, or the maternally inherited plastid genomes reveal different tree topologies than the nuclear genome data. Thus, the nuclear genome itself often has a mosaic composition due to hybridity. Integrative classification concepts, also regarding cytology, ecology, biogeography, and other datasets are needed (Karbstein *et al.*, 2024). Most agamic complexes are thought to have originated due to secondary contact hybridizations in the Pleistocene, and are evolutionarily young (Carman, 1997); therefore, relationships between taxa are shallow, and a good representation of highly resolving genomic markers is required to disentangle relationships and genetic structure of apomictic taxa. Apomictic lineages belong to taxonomically complex groups (TCGs) where artificial intelligence tools could help for classification (Karbstein *et al.*, 2024).

Biogeographical and ecological patterns suggest that apomictic taxa occupy larger and more northern distributions than their sexual relatives (Bierzychudek, 1985; Hörandl, 2006). The ability of uniparental reproduction and side effects of polyploidy enabling apomictic plants to conduct ecological niche shifts are probably the major drivers for these patterns (Hörandl, 2023). The relationships of apomixis to environmental factors are not just adaptive; in fact, different physiological responses of the plant to climatic or other abiotic stressors appear to be a trigger, or at least a modulator for the expression of naturally occurring apomixis (Hjelmqvist and Grazi, 1964; Klatt *et al.*, 2016; Klatt *et al.*, 2018; Karunaratne *et al.*, 2020; Mateo de Arias *et al.*, 2020; Ulum *et al.*, 2020). The functional background and genetic control of apomixis is complex, and most contemporary authors agree on a strong epigenetic component related to stress response of plants (Grimanelli, 2012; Léon-Martínez and Vielle-Calzada, 2019; Schmidt, 2020) as a factor for the expression of apomixis. Abiotic stress conditions would rather stimulate sexual reproduction by reactive oxygen species (ROS)-induced initialization of meiosis, whereas low-stress conditions favor asexual reproduction (e.g. Ulum *et al.*, 2020; Mateo de Arias *et al.*, 2020). Polyploids can regulate stress better than diploids (Fox *et al.*, 2020; Van de Peer *et al.*, 2021), and hence better buffered stress conditions in polyploid plants would favor apomictic reproduction (Hörandl and Hadacek,

2013). This theory is in line with the observed variation of facultative apomixis and the prevalence of polyploidy in apomictic plants. However, the different genomic factors (hybridity and polyploidy), genetic regulators (gene loci) and epigenetic components are not exclusive factors, they probably act in combination in a “regulatory landscape” of apomixis, with variable proportions of these factors in the respective developmental pathways (Léon-Martínez and Vielle-Calzada, 2019). The induction of artificial apomixis via mutant approaches or gene editing in crops differs fundamentally from natural origins of apomixis and is beyond the scope of this review (see e.g. Scheben and Hojsgaard, 2020).

The abundance and wide distribution of apomictic plants require well-founded and practicable classifications. The diversity of evolutionary processes connected to apomixis, and the methodical challenges to recognize distinct lineages (see above), has led to many different opinions regarding species delimitation, and various approaches exist to classify lineages as species, nothotaxa or as a subspecific category (Majeský *et al.*, 2017; Hörandl 2018; 2022). Therefore, most surveys on apomixis are restricted to the level of genera (Carman, 1997; Hojsgaard *et al.*, 2014a). Within genera, different specific taxonomic concepts exist, depending on the mode and stability of apomixis, the evolutionary origin and biogeography of the respective taxa (Hörandl, 2018). A recent survey on apomixis to the level of species used a pragmatic approach by considering accepted taxonomic concepts within genera as valid, and placed the question whether a unique, universal species concept for all apomictic lineages would be practicable (Hojsgaard and Pullaiah, 2023). The progress in the application of genetic and genomic data makes it nowadays possible to recognize the genetic structure of apomictic taxa and to disentangle their relationships.

In this review we focus on the progress in understanding evolution and phylogenetic patterns of apomixis in angiosperms. An update of occurrences of apomixis in orders, and families of angiosperms since Hojsgaard and Pullaiah (2023) will provide a phylogenetic framework. By reviewing selected families and genera expressing apomixis, and with detailed discussion of breeding systems, mode of apomixis, cytology, evolution, phylogeny, and taxonomy of well-studied genera, we intend to provide a better overview on the evolutionary dynamics and species-level diversity that is associated with apomixis. With this overview, we will discuss options of unified taxonomic concepts and perspectives for further research.

## II. Taxonomic distribution and diversity of apomixis in angiosperms: an update

Apomixis appears scattered in the phylogeny of angiosperms, and in all major groups (basal angiosperms, monocots, dicots). The character evolution study on the phylogeny of orders by Hojsgaard *et al.* (2014a) indicates pure sexuality as the ancestral trait in angiosperms, with shifts to apomixis occurring in several clades, and some possible reversions from apomixis to pure sexuality in terminal branches of the phylogeny. Hojsgaard *et al.* (2014a) listed the occurrence of apomixis in 30 orders, 78 families, and 292 genera (following classification of Angiosperm Phylogeny Group III (Bremer *et al.*, 2009)). The details of this literature survey were made available in an online database ([www.apomixis.uni-goettingen.de](http://www.apomixis.uni-goettingen.de)). Later, Hojsgaard and Pullaiah (2023) discriminated the occurrence of apomixis to the species level with reliable evidence of apomixis in 32 orders, 73 families, and 284 genera (following the classification of APG IV (Byng *et al.*, 2016) and Stevens (2020)); Hörandl (2024) updated to 74 families and 299 genera. The discrepancies in numbers are mostly due to different taxonomic circumscriptions.

Detection of apomixis can be done with various methods, depending on the type of apomixis (review in Hojsgaard and Pullaiah, 2023). New findings of gametophytic apomixis are most efficiently detected by large-scale screenings via the flow cytometric seed screening (FCSS) method (Matzk *et al.*, 2000), which gives information on both apomeiosis and parthenogenesis, i.e. functional seed formation. The rationale is that after apomeiosis, all nuclei in the embryo sac are unreduced, thereby doubling also the ploidy level of polar nuclei (subsequently endosperm nuclei) relative to the egg cell (subsequently forming the embryo with or without fertilization). However, interpretation of FCSS data requires information on the type of embryo sac development (Haig, 2020), because the number of polar nuclei is crucial for interpreting the endosperm ploidy and consequently the ratio to embryo ploidy (Table 1). Moreover, interpretation of FCSS patterns can be difficult to interpret in cases of autonomous apomixis, because the embryo:endosperm ratio is 1:2, which resembles in histograms also G2 peaks of mitotically dividing cells of the growing embryo. This problem appears often in Asteraceae and Plumbaginaceae (*Limonium*) where autonomous endosperm formation is common, and endosperm is rapidly consumed (Noyes, 2007; Róis *et al.*, 2016). In most other families, autonomous endosperm is uncommon because it causes strong deviations from

**Table 1.** Expected embryo and endosperm ploidy levels for sexual reproduction and most frequent developmental pathways of gametophytic apomixis in angiosperms, as detected by FCSS (Matzk *et al.*, 2000).

	Egg	Sperm nucleus	Embryo	Polar nuclei	Sperm nucleus	Endosperm	Ratio endosperm/embryo (PI)	Mode of reproduction
<b>Monosporic embryo sacs</b>								
Polygonum type (2 polar nuclei)	1	1	<b>2</b>	2	1*	<b>3</b>	1.5	sexual
Hieracium, Ixeris, Taraxacum, Antennaria, Setaria, Paspalum types (2 polar nuclei)	1 2	0 0	<b>1</b> <b>2</b>	2 4	0 0	<b>2</b> <b>4</b>	2.0 2.0	haploid parthenogenesis** autonomous apomictic
Panicum, Eragrostis types (1 polar nucleus)	2 2 2	0 1 0	<b>2</b> <b>3</b> <b>2</b>	4 4 2	1 2* 1	<b>5</b> <b>6</b> <b>5</b>	2.5 3.0 1.7	pseudogamous apomictic pseudogamous apomictic B <sub>III</sub> hybrid**
	2	0	<b>2</b>	2	0	<b>2</b>	1.0	autonomous apomictic
	2	0	<b>2</b>	2	2	<b>4</b>	2.0	pseudogamous apomictic
	2	1	<b>3</b>	1	1	<b>3</b>	1.0	B <sub>III</sub> hybrid**
<b>Bisporic embryo sacs</b>								
Allium type (2 polar nuclei)	1	1	<b>2</b>	2	1*	<b>3</b>	1.5	sexual
Ixeris type (2 polar nuclei)	2	0	<b>2</b>	4	0	<b>4</b>	2.0	autonomous apomictic
	2	1	<b>3</b>	4	1	<b>5</b>	1.7	B <sub>III</sub> hybrid**
<b>Tetrasporic embryo sacs</b>								
Drusa, Adoxa types (2 polar nuclei)	1	1	<b>2</b>	2	1*	<b>3</b>	1.5	sexual
Gagea ova type (1 polar nucleus)	1	1	<b>2</b>	1	1	<b>2</b>	1.0	sexual
Rudbeckia type (2 polar nuclei)	2	0	<b>2</b>	4	0	<b>4</b>	2.0	autonomous apomictic
Fritillaria-type (2 polar nuclei: 1n + 3n)	1	1	<b>2</b>	4	1	<b>5</b>	2.5	sexual
Penaea type (4 polar nuclei)***	1	1	<b>2</b>	4	1	<b>5</b>	2.5	sexual
	2	0	<b>2</b>	8	0	<b>8</b>	4.0	autonomous apomictic
	2	0	<b>2</b>	8	1	<b>9</b>	4.5	pseudogamous apomictic
	2	0	<b>2</b>	8	2	<b>10</b>	5.0	pseudogamous apomictic
	2	1	<b>3</b>	8	1	<b>9</b>	3.0	B <sub>III</sub> hybrid**

Here we present calculated values to show the rationale of FCSS, actual measures and peak indices usually vary a bit around the expected values. Note that values depend on the type of embryo sac development. Ploidy levels are in FCSS studies given as C or C<sub>x</sub> values (DNA content). C values here are based on diploid mother plants (for polyploids, values have to be multiplied). \*optimal 2:1 ratio of maternal: paternal genome contributions in the endosperm, pollen reduced; \*\*examples of partial apomixis, characterized by different ploidy levels of embryo compared to mother plant; generally, these are very rare reproductive pathways. \*\*\*Sometimes more than 4 polar nuclei occurs and the interpretations of reproductive pathways are therefore different. PI=peak index (endosperm/embryo). Note that peak indices depend on developmental pathway. See text and Supplement 1 for discussion of critical FCSS reports.

the optimal 2:1 maternal to paternal genome contributions in endosperm, which has negative effects on seed formation (e.g. Spielman *et al.*, 2003). For such FCSS results, independent evidence of apomixis is required. In cases of Panicum-type or Eragrostis-type embryo sacs, both containing only one polar nucleus, pseudogamous apomixis cannot be discriminated from sexual development (Hojsgaard and Pullaiah, 2023; see Table 1). Furthermore, cases of partial apomixis can be misinterpreted because they result in ploidy shifts of the embryo and in intermediate embryo:endosperm ratios (Table 1). Assessing independently the ploidy level of the mother plant to compare to the seed embryo, and careful documentation of histograms are essential for correct interpretation of such FCSS

data. Genome contributions from unreduced sperm nuclei and endopolyploidy in endosperm can further complicate interpretations of FCSS histograms. A combination of FCSS with progeny genotyping can provide more reliable information on mode of reproduction (Šarhanová *et al.*, 2024). Sporophytic apomixis still requires microscopic analyses of embryo development and/or molecular progeny tests, and in fact most questionable cases in Hojsgaard and Pullaiah (2023) belong to this developmental pathway.

Apomixis shows a clear tendency to species-rich families or subfamilies, and follows general biodiversity trends across climatic zones, with most apomicts (in absolute numbers) occurring in the Tropics (Hojsgaard *et al.*, 2014a). Overall, no major changes



have been observed in the taxonomic distribution and phylogenetic position of apomictic taxa between both surveys. Angiosperm phylogeny group IV (Byng *et al.*, 2016) recognized five small new orders, all without apomixis. On the level of orders, apomixis was newly recognized for Oxalidales with Cunoniaceae (*Davidsonia*; Elliott *et al.*, 2014) and Oxalidaceae (*Oxalis*; Doust *et al.*, 1981), and for Pandanales with Pandanaceae (*Pandanus*; Cox, 1990); after Hojsgaard and Pullaiah (2023). A further candidate appeared within the Commelinales in the family Huanguanaceae, in which apomixis is very likely according to population genetic data (Niissalo *et al.*, 2020). On the level of families, Hojsgaard and Pullaiah (2023) added Gentianaceae (*Schultesia*; Ramirez and Brito, 1990) in Gentianales. Biebersteiniaceae may be added in the Sapindales, in which gametophytic apomixis was reported for *Biebersteinia odora* by using flow cytometric seed screening (Brožová *et al.*, 2019); see Supplement 1 and Yamamoto *et al.*, 2014 why we regard this case as questionable. A further candidate for a new family would be Bromeliaceae (Poales), in which apomixis was inferred from bagging and emasculation experiments; however, the authors of this survey point at weaknesses of the methodical approach and the difficulties to discriminate pseudogamous apomixis from self-fertility (Cascante-Marín and Núñez-Hidalgo, 2023). Similar concerns hold for a record for Lamiaceae (*Thymus*, Orellana *et al.*, 2005; see Supplement 1). New reports of gametophytic apomixis were presented for Montiaceae (*Claytonia*), Schoepfiaceae (*Arjona*), and Geraniaceae (*Geranium*) based on FCSS by Ptáček *et al.*, (2024), but remain doubtful without documentation of embryo sac development, ploidy levels, and flow cytometric histograms (Supplement 1). The re-investigation of older records by Hojsgaard and Pullaiah (2023) led to doubt for apomixis occurrences in Adoxaceae, Caprifoliaceae, Caricaceae, Cyrillaceae, Dioscoreaceae, Lecythydaceae, Onagraceae, Paeoniaceae, and Sapindaceae. For new records on genus level see family treatments below, Hojsgaard and Pullaiah (2023), and Hörandl (2024). Apomictic reproduction has recently been suggested for two polyploid taxa of species-rich genus *Senecio* (Asteraceae) from Australia, based on unusual pattern of genetic variation (Ahrens and James, 2015), but later FCSS analyses revealed full sexuality of overrepresented multilocus genotypes, thus refuting apomixis in these species (Mráz *et al.*, 2024). Overall, the new findings confirm results by Hojsgaard *et al.* (2014a) that apomixis occurs mostly in diverse families and genera. There is no apparent general geographical trend to a certain climatic zone, but new findings

appear to be more likely in less investigated geographical areas, like the Himalayas (Brožová *et al.*, 2019) or the Neotropics (Souza-Pérez and Speroni, 2017). The update of apomixis occurrences at levels of orders and families do not show significant patterns of clustering (Figure 1).

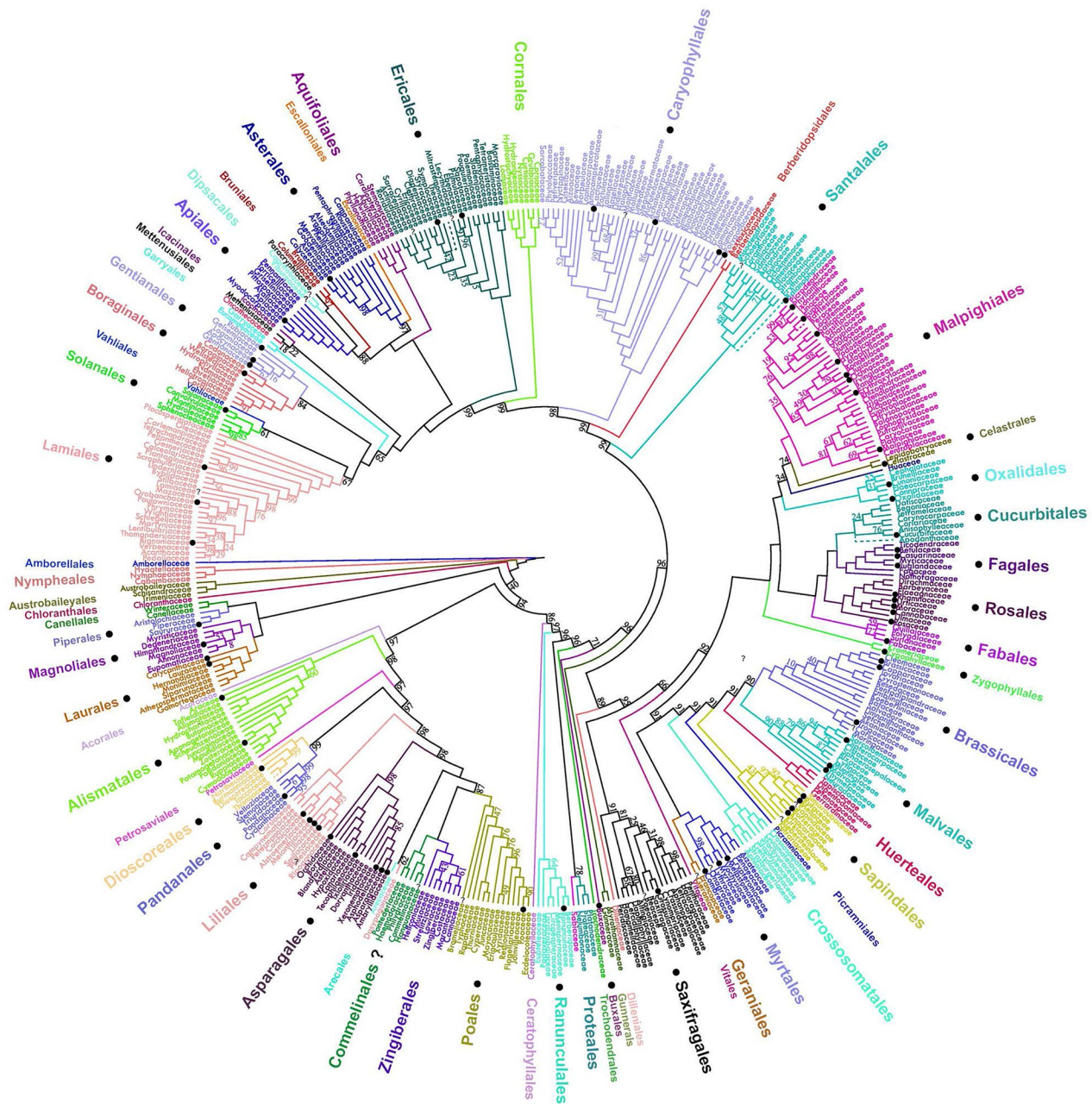
It remains an open question whether the clustering of apomixis in certain plant families (mainly Asteraceae, Poaceae, and Rosaceae) would be due to genetic or developmental predispositions (Van Dijk and Vijverberg, 2005). Somatic plant cells can be readily re-programmed by transcription factors and epigenetic factors to become totipotent, as known e.g. from somatic embryogenesis (Su *et al.*, 2021). Under this aspect, shifts to apomixis appear feasible for all angiosperms. Carman (1997) postulated a correlation of apomixis to other developmental abnormalities - like polysporous embryo sacs, which could be a remnant of ancient apomixis after a return to sexuality in certain lineages. This theory would see apomixis mostly as a transitional phase during polyploidization, with a return to sexuality. Reversals from asexuality to sexuality are in principle possible (Hörandl and Hojsgaard, 2012) and were also documented in phylogenies of animals (Domes *et al.*, 2007). However, for angiosperms it appears that many different evolutionary pathways are possible to shift between modes of reproduction.

### III. Monocots

#### A. Poaceae

The grass family represents a diverse group of species adapted to a wide range of geographic areas and climatic regions whose species can be found on every continent (<https://www.mobot.org/MOBOT/Research/APweb/welcome.html#Famlarge>). Apomixis in grasses was first recorded in species of *Poa* (Zollikofer, 1930; Müntzing, 1933) and *Calamagrostis* (Stenar, 1932).

Sporophytic or gametophytic apomixis is detected in more than 240 grass species and 56 genera, making it the family with the greatest number of apomictic genera (Hojsgaard and Pullaiah, 2023). Previous works listed about 250 species with apomixis belonging to the Poaceae (Pullaiah and Febulaus, 2000). Despite the finding of new apomictic grasses during the last two decades, the difference with the most recent and the previous surveys is largely due to taxonomic changes in species classification (as mentioned above). Sporophytic apomixis in the form of nucellar embryony has been rarely observed in genera such as *Bothriochloa* (Moskova, 1975), *Cenchrus*



**Figure 1.** Phylogeny of the families and orders of angiosperms. Tree topology and bootstrap percentages (only less than 100 shown at branches) after Li *et al.*, (2021), published Open access under a Creative Commons Attribution 4.0 International License; orders added after Angiosperm Phylogeny group IV (Byng *et al.*, 2016) and in the same color as the respective families. Occurrences of apomixis are indicated with black dots at the family/order name, questionable records with question marks; records after Hojsgaard and Pullaiah (2023) and the text here (see also Supplement 1).

(Shanthamma and Narayan, 1976), *Eulaliopsis* (Yao *et al.*, 2007) or *Poa* (Batygina, 1991). Gametophytic apomixis in the form of diplospory is common among species of genera such as *Calamagrostis* (Greene, 1984), *Cenchrus* (Dujardin and Hanna, 1984), *Eragrostis* (Voigt and Bashaw, 1972) or *Tripsacum* (Farquharson, 1955), to mention a few. Gametophytic apomixis in the form of apospory is common among species of genera such as *Bothriochloa* (Brown and Emery, 1958), *Brachiaria* (do Valle and

Glienke, 1991), and *Paspalum* spp. (Ortiz *et al.*, 2013). In *Poa*, species with apomixis and/or diplospory have been recorded (Nygren, 1950a, b). In *Stipa*, gametophytic apomixis has been inferred from FCSS (Brožová *et al.*, 2019). In most genera, apomixis is well documented and has been confirmed through embryological and FCSS analyses. A detailed list of apomictic species and diversity of developmental pathways for apomixis have been presented elsewhere (Hojsgaard and Pullaiah, 2023).

Thus, apomixis has arisen in the two major clades within the family, the PACMAD clade and the BOP clade. Examples to the PACMAD clade belong *Eragrostis* or *Chloris* from the subfamily Chloridoideae; *Cortaderia* and *Danthonia* belong to the subfamily Danthonioideae; and *Bothriochloa*, *Brachiaria*, *Cenchrus*, and *Paspalum* belong to subfamily Panicoideae. To the BOP clade belong *Calamagrostis* and *Poa* from the subfamily Pooideae. The more basal lineages within the family, i.e. the subfamilies Anomochlooideae, Pharoideae, and Puelioideae contain few species (Soreng *et al.*, 2017) and apomixis has not been recorded (Hojsgaard and Pullaiah, 2023).

Detailed biogeographic studies in grass genera containing apomictic species are not rare (see e.g., Arthan *et al.*, 2022; Gallaher *et al.*, 2022), but in most cases, they are not focused on apomictic species as this requires additional information on ploidy or genome sizes and reproductive biology. Despite such information being useful, it requires often neglected cytological skills and knowledge. For instance, a recent study on the phylogeny and biogeography of *Calamagrostis* (Peterson *et al.*, 2022) included 9 out of 10 apomictic species listed by Hojsgaard and Pullaiah (2023) but without referencing ploidy or reproductive mode. The phylogenetic schemes inferred from Bayesian analyses of ITS and plastid data from species representing multiple origins and uncertain phylogenetic positions (Peterson *et al.*, 2022) included eight of those putatively apomictic species. Polyploidy and apomixis are known to generate conflicting topologies due to incongruent signals between markers or confounding sequences (multiple alignments) (see below).

Another reason to avoid including ploidy and reproductive mode data in phylogenetic analysis of apomictic grasses is likely connected to the challenges imposed by rather low morphological variability and the occurrence of polyploidy, hybridization, and apomixis that hamper proper taxonomic analyses. In this sense, the species concept used by taxonomists to delimitate apomictic grass species has followed the most operational concept in practice, i.e. the use *a priori* of a traditional phenetic concept combined to alternative molecular markers in attempts to provide a theoretical background for *a posteriori* species delimitation. The recognition of apomictic species or lineages and their relationships cannot be defined by phenetic traits alone and additional criteria of species are required (Hörandl, 2022). For some years now, “integrative taxonomy” or the use of multiple perspectives like phylogeography, comparative morphology, population genetics, ecology, cytology, development, etc. has been proposed to delimit the units of life’s diversity (Dayrat, 2005). Yet,

systematic and taxonomic studies that integrate information from different fields have rarely been used in apomictic grasses.

Chromosomal change plays a central role in the evolution of the family. An ancestral karyotype with a minimal size of 33.6 Mb structured in five proto-chromosomes was suggested for the family based on gene order and content (Salse *et al.*, 2009). The major evolutionary shuffling events of whole-genome doubling (WGD) and diploidization, followed by lineage-specific rearrangements, explain the extant diversity of chromosome numbers and genome divergence (Bolot *et al.*, 2009). In addition, synteny break-points and junction sequences had provided evidence of the molecular mechanisms driving chromosome shuffling events. Today’s chromosomal variation/reduction from the  $n=12$  common paleo-ancestor to grass subfamilies with and without apomixis (e.g. Pooideae and Ehrhartoideae of the BEP clade, and Panicoideae of the PACMAD clade) was driven by nonrandom centromeric/telomeric illegitimate recombination between nonhomologous chromosomes causing nested chromosome fusions and synteny break points (Murat *et al.*, 2010). Such structural but also functional (i.e. neo- or subfunctionalization) changes following WGD provided polyploids with competitive advantages such as increased vigor, wider environmental tolerance, self-fertilization, and formation of apomictic species, all promoting the ability to establish new lineages and adapt to conditions not tolerated by their diploid ancestors (Murat *et al.*, 2010; Hojsgaard, 2018). The absolute contribution of each of these traits, including apomixis, to macroevolutionary processes has yet to be revealed.

Previous analyses have shown an association between the presence of apomixis and higher numbers of species and genera among the subfamilies of Poaceae, Asteraceae, and Orchidaceae (Hojsgaard *et al.*, 2014a). In large, diverse, and genomically complex genera, (allo- and auto-) polyploidy, hybridization, and apomixis are key players of diversification and geographic distributions. Within the Poaceae, *Paspalum* is perhaps the genus with most studies involving apomixis and might therefore serve as a case study about undergoing natural processes and methodical issues in the taxonomic and phylogenetic analyses among apomictic grasses.

### 1. *Paspalum*

In *Paspalum*, a genus of 10.6 My old, (Burke *et al.*, 2018) with ca. 350 species, many of them apomictic, phylogenetic relationships among species are partially



recovered due to reticulation events, frequent autopolyploidization (but also allopolyploidization) and apomixis, obscuring infrageneric classification (Scataglini *et al.*, 2014). *Paspalum* species are mainly American and ecologically diverse. Apomictic species are not restricted to a specific ecoregion and can be found in a variety of environments from the Atlantic to the Pacific (Zuloaga and Morrone, 2005), from seashore species that specialize on saline habitats (halophytes) like *P. vaginatum* and *P. distichum* (Goad *et al.*, 2021) to macrophytes like *P. modestum* and *P. repens* (Karunaratne *et al.*, 2020a) or mountain species like *P. remotum* and *P. volcanense* (Glücksberg *et al.*, 2019).

Sexual species are allogamous, with a few exceptions, and develop Polygonum-type embryo sacs (Ortiz *et al.*, 2013). Apomixis is expressed as apospory in most species, rarely diplospory, through the development of 4-nucleate *Paspalum*-type or 8-nucleate Hieracium-type and Taraxacum-type embryo sacs (Hojsgaard and Pullaiah, 2023). As most apomicts from different grass genera, *Paspalum* apomicts are polyploid, self-fertile and pseudogamous. Seed set among apomicts is often lower than in sexuals (e.g. Hojsgaard *et al.*, 2016) but self-fertility and pseudogamy provide apomicts the ability of uniparental reproduction (Reutemann *et al.*, 2022).

In model species such as *P. notatum* and the *Anachyris* group (*P. simplex*, *P. malacophyllum* and *P. procurrens*), the locus or loci controlling apomixis are in low-recombination or nonrecombining regions, which prevents precise identification of associated genes. This region spans at least 6 cM and several megabases (Pupilli *et al.*, 2004; Hojsgaard *et al.*, 2011). Similar findings in apomictic grasses belonging to other like *Urochloa* or *Pennisetum* (Akiyama *et al.*, 2004; Worthington *et al.*, 2016) indicate this might be a common feature in the origin of apomixis among species of the tribe Paniceae in the subfamily Panicoideae. Developmental steps in apomictic ovules are asynchronous and exhibit a general gene de-regulation compared to sexual ones (Hojsgaard *et al.*, 2013; Ortiz *et al.*, 2020). Genetic mapping, cloning, and gene expression analyses have identified genes with diverse functions during apomixis (Hojsgaard, 2020; Ortiz *et al.*, 2020), but none of them is specific for the avoidance of meiosis or parthenogenesis. Apomixis is in *Paspalum* highly facultative, particularly at early developmental stages, and influenced by environmental conditions (Quarin, 1986; Karunaratne *et al.*, 2020b).

Autopolyploidy has a major role in the evolution of apomictic complexes in the genus, while

hybridization and allopolyploidy have produced a few lineages. Most species have sexual self-sterile diploids and apomictic self-fertile tetraploids, but other ploidy combinations also occur as well as species with one ploidy level (Ortiz *et al.*, 2013). In diploids, the spontaneous formation of unreduced embryo sacs at very low frequencies (e.g. Norrmann *et al.*, 1989; Hojsgaard *et al.*, 2008) is a regular mechanism and is key for polyploidization. Polyploids in these complexes have arisen multiple times from different populations throughout the main genetic clusters of diploids, and because of apomixis, polyploids have less genetic structure, meaning a smaller amount and more fragmented distribution of genetic variation within and between populations (Karunaratne and Hojsgaard, 2021). Such polyploidization dynamics have contributed to widen their geographic distributions. At least in some species, geographic displacement between cytotypes in contact zones promoted their ecological differentiation (Karunaratne *et al.*, 2018) and shaped the observed patterns of cytotype distribution in these agamic complexes, often exhibiting geographical parthenogenesis (Quarin and Lombardo, 1986; Urbani *et al.*, 2002; Karunaratne *et al.*, 2018). Because of the recurrent origins and autopolyploidy, many agamic cytotypes are included into one species together with sexuals and show low or no intraspecific morphological variation (e.g. Karunaratne and Hojsgaard, 2021). Classification of species is thus only challenged by high phenotypic plasticity and overlap in species morphologies, which happen in a few cases, like in *P. malacophyllum* or *P. alnum* (Chase, 1933). In the latter, a diploid cytotype described as a different species, *P. hexastachyum*, was later synonymized to tetraploid *P. alnum* based on cytotaxonomic and embryological analyses, and resynthesis of polyploids by colchicine (Quarin, 1974; Quarin and Hanna, 1980). Morphological and ecological similarities among species have driven taxonomists to create infrageneric informal groups (Chase, 1929), and analyses show that these are phylogenetically unsupported, artificial groups of polyphyletic origins (see e.g. Denham *et al.*, 2010; Delfini *et al.*, 2023). In species from a few informal groups like *Plicatula*, *Stellata* or *Dilatata*, hybridization plays an active role creating a reticulate pattern in which morphological or genetic delimitation of taxa is not possible and are therefore, taxonomically challenging (see e.g. Oliveira, 2004; Bonasora *et al.*, 2015).

So far, phylogenetic studies in the genus have partially resolved species relationships while species delimitation in some clades remains unclear (Giussani *et al.*, 2009; Rua *et al.*, 2010; Scataglini *et al.*, 2014).

Next-generation sequencing (NGS) methods, specifically reduced representation methods like RAD-Seq (Restriction site-associated DNA sequencing), have become popular to visualize tree topologies on shallow phylogenetic levels (see e.g., Hörandl, 2022). In *Paspalum* and among grass species from other apomictic genera like *Urochloa* or *Eragrostis*, NGS methods have so far not been used for phylogenetic purposes, but to reveal genome (structures and) evolution in species of agronomic interest (e.g. Tomaszewska *et al.*, 2023).

New attempts to resolve species relationships in *Paspalum* and grass genera with polyploidy, hybridization, and apomixis might greatly benefit from integrative approaches collecting data not only from morphology or anatomy (quantitative/qualitative traits) and genetics (markers, sequences), but also from cytology (basic chromosome numbers, ploidy, molecular cytogenetics), embryology (types of sexual or apomictic development), reproductive biology (pollination syndrome, phenology), and ecology (ecological niche, distribution).

## IV. Dicots

### A. Ranunculaceae

The Ranunculaceae are the only family in Ranunculales exhibiting apomixis, with records for the following three genera: *Thalictrum* (Overton, 1902; Daskalova, 2004), *Ranunculus* (Häfliger, 1943; Nogler, 1984b; 1995; Hojsgaard *et al.*, 2014b) and *Halerpestes* (Brožová *et al.*, 2019). For the dioecious species *Thalictrum purpurascens*, the developmental pathway is not completely clear (Overton, 1902), whereas for *T. aquilegifolium* nucellar embryony has been documented (Daskalova, 2004). Gametophytic apomixis is best documented in various species of *Ranunculus* (see below). Old records of suspected apomixis in *Ficaria* (Metcalf, 1939) remain unsupported so far (Popelka *et al.*, 2019). Records of autonomous apomixis for *Caltha* based on FCSS only (Ptáček *et al.*, 2024) need confirmation because apomictic Ranunculaceae usually reproduce via pseudogamy (based on 8-nucleate embryo sacs with 2 polar nuclei, Johri *et al.*, 1992; see below under *Ranunculus*).

The pattern confirms the emergence of both forms of apomixis (sporophytic and gametophytic) in distantly related major clades of the family: *Thalictrum* belongs to subfam. Thalictrioideae, *Ranunculus* and *Halerpestes* belong to Ranunculoideae (Cossard *et al.*, 2016). In the phylogeny of *Ranunculus* and related genera (tribe Ranunculeae), apomixis emerges four

times in different clades, suggesting a convergent and derived evolution of the trait. It is unclear whether any predispositions for apomixis can be assumed in tribe Ranunculeae. From a genomic and chromosomal perspective, it may be noteworthy that all the apomictic taxa have the same ancestral karyotype of four metacentric and four submetacentric/subtelocentric chromosomes. This so-called “Bauer” karyotype occurs in most species of the basal clades (Baltisberger and Hörandl, 2016), whereas the more derived clades of *Ranunculus* (subgenus *Ranunculus*) exhibit a higher variation of karyotypes and chromosome types. Eventually, uniform karyotypes in the basal part of the phylogeny facilitated the frequently observed interspecific hybridization as a potential trigger for apomixis (Baltisberger and Hörandl, 2016). Ecologically, *Halerpestes lancifolia*, *R. parnassifolius*, and *R. kuepferi* are alpine species, whereas the *R. auricomus* complex occurs more in lowlands and reaches just subalpine vegetational zones; the latitudinal spectrum ranges from the Mediterranean to the Arctic. A clear correlation of apomixis to cold climates was just shown for *R. kuepferi* in the European Alps (Schinkel *et al.*, 2016), but not for the widespread *R. auricomus* complex (Karbstein *et al.*, 2021).

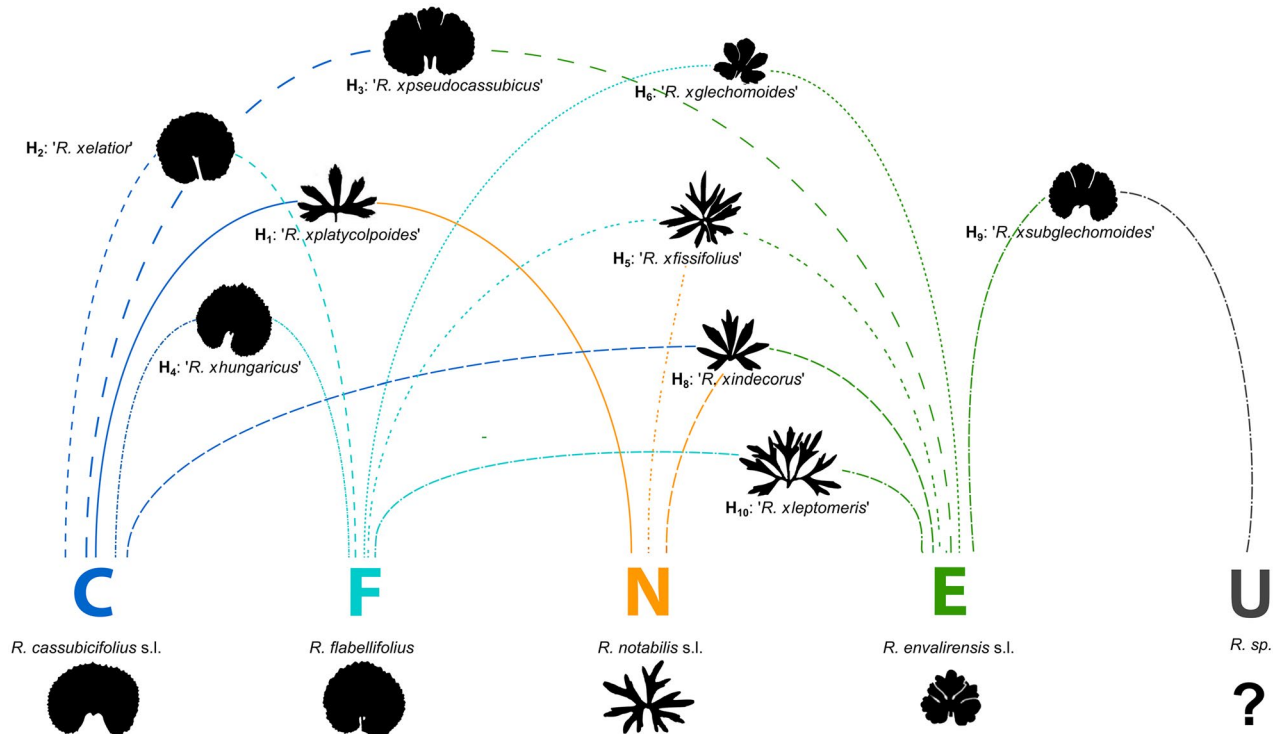
### 1. *Ranunculus*

The genus *Ranunculus* comprises c. 600 sexual species and has a worldwide distribution (Emadzade *et al.*, 2011). Specifically, the Eurasian *R. auricomus* complex is regarded as a model system for development and evolution of apomixis. Sexual *Ranunculus* has Polygonum-type embryo sacs as typical for Ranunculaceae, and apomixis is expressed as apospory, with aposporous initials appearing at the end of megasporogenesis (during the tetrad stage) and replacing the aborting megaspore. Further development of the aposporous initials results in an 8-nucleate embryo Hieracium-type embryo sac, with parthenogenetic development of unreduced egg cells into an embryo (Nogler, 1984a; 1984b). Usually, pollen is needed to fertilize the polar nuclei (pseudogamy) for proper development of the endosperm and fertile seed formation (e.g. Hojsgaard *et al.*, 2014b; Klatt *et al.*, 2016; Schinkel *et al.*, 2016). Pollen fertility is reduced, but still functional pollen is left for pseudogamy, whereby self-pollen is also functional in the apomictic plants (Hörandl, 2008) and provides apomicts the ability of uniparental reproduction. Nogler (1984a; 1995) established that apospory is under genetic control and inherited by a single, apospory-controlling Mendelian factor. However, it has been shown that emergence

and inheritance of apospory is also possible in diploids (Barke *et al.*, 2018). Four candidate genes for apospory were found via transcriptome sequencing and analysis of loci under selection in aposporous hybrids (Paetzold *et al.*, 2022), but the genetic basis of parthenogenesis is still unclear. Apomixis in *Ranunculus* is highly facultative and proportions of apospory are to some extent influenced by environmental conditions (Klatt *et al.*, 2016; Syngelaki *et al.*, 2020a; 2020b; Ulum *et al.*, 2020), suggesting a strong epigenetic component in the “control landscape”.

Evolution of apomictic complexes follows largely the classical scheme of Babcock and Stebbins (1938). Four diploid sexual and one tetraploid sexual progenitor species are known; these diversified from c. 700,000 years ago onwards via allopatric speciation and have restricted, disjunct current distributions (Tomasello *et al.*, 2020). Hybridization between these progenitors during range fluctuations has resulted in a huge amount of apomictic, tetraploid to hexaploid lineages with slightly different morpho- and ecotypes (Karbstein *et al.*, 2022; Figure 2). Hybridization of sexual species as a trigger for the

shift to apospory has been also documented experimentally (Hojsgaard *et al.*, 2014b; Barke *et al.*, 2018), whereby to some extent meiosis disturbances (Barke *et al.*, 2020), but also combinations of mutations in important developmental genes (Paetzold *et al.*, 2022) could be functional backgrounds. These mutations might be already present in sexual species as very rare apomictic seed formation has been observed (Karbstein *et al.*, 2021). In Central Europe facultative apomixis is still predominant, while obligate apomictic lineages have colonized Northern and Southern Europe (Karbstein *et al.*, 2021; Bradican *et al.*, 2023). The gene pools of the progenitor species shape the three main genetic clusters within the complex that show altogether an East-West differentiation in Europe. This East-West pattern extends to Siberia and the Beringian region, whereby an unknown progenitor in Central Asia could have been involved (Bradican *et al.*, 2024). However, the well-documented hybrid origin, the lack of morphological distinctness between lineages, and the local distributions favored a classification of previously described agamospecies as nothotaxa (hybrids)



**Figure 2.** Hybrid scheme of sexual progenitors and selected apomictic allopolyploid *Ranunculus auricomus* derivatives (H1–H10), inferred from RAD-Seq data and PhyloNet analyses of 48 phased nuclear genes (Karbstein *et al.*, 2022). The diploid sexual progenitor species *Ranunculus cassubicifolius* (subgenome C), *R. flabellifolius* (subgenome F), *R. notabilis* (subgenome N), *R. envalirensis* (subgenome E), and a hypothetical unknown taxon (U) in different combinations gave rise to apomictic polyploid derivatives. Differently dashed lines to the left and right specify parental subgenome contributions of allopolyploids. Subgenome dominance is shown by the relative position of the polyploid to the progenitors. Apomictic hybrids classified as nothotaxa. Reprinted from Karbstein *et al.* (2022) (copyright with the authors).

(Karbstein *et al.*, 2022; Melzheimer and Hörandl, 2022; Hodač *et al.*, 2023; Bradican *et al.*, 2023; 2024).

In the model system *R. kuepferi*, gametophytic apomixis occurs rarely in the diploid, otherwise sexual cytotype, but is predominant as facultative apomixis in the polyploid, mostly tetraploid cytotypes (Cosendai and Hörandl, 2010; Schinkel *et al.*, 2016; Klatt *et al.*, 2018). The tetraploids had multiple autopolyploid origins (Cosendai *et al.*, 2011) and emerged within the last 10,000-80,000 years (Kirchheimer *et al.*, 2018), which is in evolutionary time frames too short for substantial genetic diversification (Cosendai *et al.*, 2011). The diploids occur only in the southwestern, previously unglaciated parts of the Alps, whereas the tetraploids occur in the whole, previously glaciated and higher parts of the Alps, thus providing a classical example of geographical parthenogenesis (Cosendai *et al.*, 2013). Triploids appear in the contact zone of diploids and tetraploids. According to FCSS results, these triploids are mostly the result of ongoing polyploidization events via a female triploid bridge (Schinkel *et al.*, 2017). Experimental work suggests that unreduced female embryo sac formation might be triggered by freezing temperatures (Klatt *et al.*, 2018). After fertilization of unreduced egg cells, the resulting triploids can become tetraploids via a so-called triploid bridge. The apomictic tetraploids show a better cold acclimation to higher altitudes and cold conditions, both phenotypically and epigenetically and in gene expression (Klatt *et al.*, 2018; Syngelaki *et al.*, 2020a; 2020b; 2021). During postglacial re-colonization of the Alps, this fostered rapid spread of the tetraploid apomictic cytotype in a novel, colder ecological niche (Kirchheimer *et al.*, 2018).

Morphologically, the diploids do not differ from tetraploids except for some traits related to apomixis in the latter (reduced, incomplete corollas and low pollen quality). Based on these few features Huber (1988) classified the tetraploids as *R. kuepferi* subsp. *orientalis* whereas the diploids represent subsp. *kuepferi*. Detailed morphometric analysis of natural populations showed slightly better growth and more flowers in diploids, but these features are variable under different temperature conditions (Schinkel *et al.*, 2016; Syngelaki *et al.*, 2020a) and hence not useful for taxonomic considerations. Therefore, a classification of apomicts on species level is not justified.

Embryological investigation confirmed apospory in *R. parnassifolius* subsp. *heterocarpus* (Vuille and Küpfer, 1985), which might represent a similar case of an autopolyploid cytotype (Cires *et al.*, 2010; 2012), but mode of reproduction has not been thoroughly studied. In contrast, other high alpine buttercup

species like *R. pygmaeus*, *R. alpestris*, and *R. glacialis* are obligate sexual (Hörandl *et al.*, 2011). Gametophytic apomixis with pseudogamy has been detected via FCSS in the Himalayan taxon *R. membranaceus* (Brožová *et al.*, 2019). Other Himalayan species in this clade are good candidates for apomixis, as the Himalayan clade represents a young radiation with polyploids, reticulate evolution and unclear species delimitation (Emadzade *et al.*, 2015). Polyploidy is prevalent in Himalayan *Ranunculus* species, and pollen meiosis behavior is often abnormal, with frequent cytotoxicity (i.e. the migration of nuclei from one plant cell to another through intercellular channels) (Jeelani *et al.*, 2014). A record of autonomous apomixis in *R. peduncularis* from South America based on FCSS only (Ptáček *et al.*, 2024) requires confirmation, because pseudogamy is prevalent in all other *Ranunculus* species. Further investigations in high mountain systems of the world are promising to detect more apomictic buttercup species.

## B. Plumbaginaceae

The Plumbaginaceae (noncore Caryophyllales) family, with nearly 940 species (Caperta *et al.*, 2020), comprise two subfamilies, the Plumbaginoideae and Limonioideae (= Staticoideae) (Hernández-Ledesma *et al.*, 2015; Kubitzki, 1993; Malekmohammadi *et al.*, 2017). The genus *Limonium* (sea lavenders) included in Limonioideae, encompasses several taxonomic complexes and ca. 600 species (Malekmohammadi *et al.*, 2017; Hassler, 2018; Koutroumpa *et al.*, 2018), and is well known for apomixis (Baker, 1966; Erben, 1978; 1993; Ingrouille and Stace, 1985; 1986; Lledó *et al.*, 2005; Caperta *et al.*, 2018). The main center of species diversity is the Mediterranean basin, where it has been assumed that apomicts account for a large proportion of the species (Erben, 1978; 1993; Cowan *et al.*, 1998; Brullo and Erben, 2016). This genus is considered taxonomically complicated (Baker, 1966; Erben, 1978; 1993; Ingrouille and Stace, 1985; Lledó *et al.*, 2005; Cortinhas *et al.*, 2015; Malekmohammadi *et al.*, 2017; Caperta *et al.*, 2018; Koutroumpa *et al.*, 2018; Róis *et al.*, 2018; Pina-Martins *et al.*, 2023a; 2023b), generally accounted for a combination of several phenomena: (i) a polymorphic sexual system associated with flower polymorphism, (ii) hybridity, (iii) polyploidy, and (iv) apomixis.

### 1. *Limonium*

**The polymorphic sexual system.** In *Limonium*, as well as other Plumbaginaceae members, plants show a



polymorphic sexual system associated with striking flower polymorphisms and linked to a sporophytic self-incompatibility system (SI). Heterostyly (populations with a reciprocal arrangement of styles and anther heights, i.e. reciprocal herkogamy) is typical in members of Plumbaginoideae and rare in Limonioideae (e.g. *L. vulgare*, Baker, 1948; Cortinhas *et al.*, 2015) whereas pollen/stigma polymorphism is widespread in the genus (Costa *et al.*, 2019).

The species present heteromorphic flowers and show ancillary pollen (differences in pollen size, shape, and exine sculpturing) and stigmas (linear with papillae with distinct sizes and morphology) (Baker, 1948; 1966; Nowicke and Skvarla, 1976) that prevent self- and intramorph mating (Baker, 1948; 1966; Dulberger, 1975a; 1975b; Róis *et al.*, 2016; Conceição *et al.*, 2021). Dimorphic species have different pollen-stigma combinations: A - coarsely reticulate sexine - cob type stigma (*A/Cob*); B - finely reticulate sexine - papillate type stigma (*B/Pap*); C - finely reticulate sexine - cob type stigma (*B/Cob*); and D - coarsely reticulate sexine - papillate type stigma (*A/Pap*). A and B represent self-sterile combinations whereas C and D are self-fertile (Baker, 1966; Dulberger, 1975a; 1975b). Species with self-sterile combinations reproduce through outcrossing or apomixis (Baker, 1966; Erben, 1978).

Sexual species have anthers with pollen with high viability, but apomicts show empty anthers or few pollen grains that may present diverse morphology and sizes (Erben, 1978; 1979; Róis *et al.*, 2012; Conceição *et al.*, 2021). Sexual diploid *L. ovalifolium* ( $2n$ ) produces reduced pollen with high viability (Róis *et al.*, 2016) but triploid *L. algarvense* ( $3n$ ) (Conceição *et al.*, 2019) have pollen with low viability like tetraploid apomicts of *L. binervosum* complex (Róis *et al.*, 2016). However, SI monomorphic apomicts can show viable pollen grains that poorly adhere to stigmas (Dulberger, 1975a; 1975b; Costa *et al.*, 2019). Male-sterile species, which reproduce by apomixis, present pollen grains with a collapsed morphology but have regular stigmas (Róis *et al.*, 2012; 2016).

Here we compiled diverse species regarding ploidy, flower morphs, and apomixis type described in the literature (Supplement 2). Most species are triploid ( $n=46$ ), followed by tetraploid ( $n=17$ ), diploid ( $n=12$ ), pentaploid ( $n=4$ ), and hexaploid ( $n=3$ ) and some species ( $n=8$ ) have more than one ploidy level. From these, 16 self-incompatible (eight *A/Cob* and eight *B/Pap*) (e.g. *L. ovalifolium*), five self-compatible monomorphic species (four *B/Cob* and one *A/Pap*) and four self-compatible diploid species (three *B/Cob* and one *A/Pap*) were reported. Among triploids, one

male sterile with *cob* stigma, out of 29 self-incompatible species (12 *A/Cob* and 17 *B/Pap*) was reported. In tetraploids, fourteen self-incompatible (11 *A/Cob* and three *B/Pap*), four self-compatible (one *B/Cob* and one *A/Pap*), and five male-sterile with *cob* stigma and one male sterile with *pap* stigma were described. Only five self-incompatible pentaploids (two *A/Cob* and three *B/Pap*), and two *A/Cob* self-incompatible (e.g. *L. cythereum*) and one *A/Pap* self-compatible (*L. humile*) hexaploids were recognized. Most diploids reported so far are dimorphic, with only two reports of monomorphic species (*L. cossonianum*, *L. californicum*) (Supplement 2). Strikingly, most triploids are monomorphic ( $n=26$ ) as are some tetraploids ( $n=15$ ); however, dimorphic triploids (*L. coincyi*), tetraploids (*L. narbonense*), pentaploids (*L. roridum*) and hexaploids (*L. graecum*) were also found (Supplement 2).

**Ongoing hybridization.** The main limitation in the study of hybrid speciation in *Limonium* is the lack, among extant populations, of putative parents – or entities that could be considered as parents of the extant taxa. Recent interspecific hybrids have been reported (Erben, 1978; 1993) but there are extremely few instances that have adequate documentation. In 15-20 species of ornamental interest, interspecific crosses gave rise to a number of partially fertile hybrids, with fertility restored through somatic chromosome doubling (Morgan and Funnell, 2018).

Efforts have been made to gain insight on hybridization in the genus. Crosses between diploid species from the *L. ovalifolium* complex produced both fertile and infertile hybrids, showing maternal and paternal pollen-stigma combinations and inflorescence types or intermediate inflorescence morphotypes (Conceição *et al.*, 2021). Thus, reproductive barriers between the diploid species seem to be weak or nonexistent. In contrast, crosses between tetraploids and diploids from distinct species complexes failed to produce true hybrids and progeny arose via apomixis, with high levels of developmental anomalies in seedlings like pleiocotyly (more than two cotyledons per seed) and polyembryony (more than one embryo per seed) (Conceição *et al.*, 2018; 2021). Remarkably, despite the lack of hybrids, bidirectional pollen transport by insect visitors was observed between sexual and apomictic plants, meaning that intercytotype mating and gene flow can occur (Conceição *et al.* 2021).

**Apomixis.** *Limonium* has a high incidence of polyploidy (Erben, 1978; 1979; Castro and Rosselló, 2007; Caperta *et al.*, 2018; Marques *et al.*, 2018). Diploid species ( $2n=16$  or  $2n=18$ ) seem to be cytologically stable,

with typically two basic chromosome numbers,  $x=8$  and  $x=9$  (Erben, 1978) and sexual reproduction (Supplement 2). Apomixis is usually inferred by a combination of the occurrence of odd ploidy, aneuploidy, and monomorphic plants with self-incompatible combinations that produce seeds (Erben, 1978; Ingrouille and Stace, 1985; 1986; Cowan *et al.*, 1998). Thus, all inferred apomicts in the literature are polyploid, and sexual species may present a low expressivity of apomixis (e.g. *L. ovalifolium*, Róis *et al.*, 2016).

Although in *Limonium* there are very few polyploid taxa for which at least one parent has been hypothesized or recognized with high likelihood (Erben, 1978), the evolutionary history of most taxa is unknown. Based on morphology, karyotype differences and embryology, Erben (1978; 1993) proposed parental species for several polyploid hybrids, and suggested that polyploid taxa originated from parents with different combinations of the basic chromosome numbers  $x=8$  and  $x=9$ , but this hypothesis is not yet proven. Triploids are by far the predominant cytotype among *Limonium* spp. in the Iberian Peninsula and the Balearic Islands (Erben, 1978; 1979; Cowan *et al.*, 1998; Castro and Rosselló, 2007), like the allotriploid apomict *L. dufourii* (Palop-Esteban *et al.*, 2007). Polyploids from the *L. vulgare* complex show diverse breeding systems, such as the sexual autopolyploid *L. narbonense* (Palop-Esteban *et al.*, 2011), and the sexual hexaploid *L. humile* (Dawson and Ingrouille, 1995) and the putative apomict *L. maritimum* (Cortinhas *et al.*, 2015) occurring in a wide spectrum of environmental conditions and in sympatry with related species (Pina-Martins *et al.*, 2023).

Other studies hypothesizing the parental origin of polyploid species in *Limonium* are only based on unreliable morphological characters. For example, *L. algarvense* is considered a homogeneously triploid taxon ( $2n=3x=25$ ) that originated from crosses between diploid sexual *L. ovalifolium* and tetraploid apomict *L. binervosum* (Ingrouille, 1985). Nonetheless, these two species do not occur in sympatry as tetraploid apomicts are distributed at higher latitudes (37–55°N) than diploid sexuals (34–48°N), and triploid *L. algarvense* thrives in the southern boundaries of diploids (35–39°N) (Caperta *et al.*, 2017). Ecological differentiation was also found between the *L. ovalifolium* and *L. binervosum* complexes and *L. algarvense*, namely in the frequency of occurrences on the most common lithological groups (Caperta *et al.*, 2017). While *L. algarvense* occurs more frequently on alluvial sediments in deltas, the *L. ovalifolium* complex shows preferences on limestone rocks, and the *L. binervosum*

complex occurs on alluvial deposits, limestones and till sites (Caperta *et al.*, 2017). These species show variations in genome size, chromosome numbers, and meiotic behavior (Caperta *et al.*, 2017; Conceição *et al.*, 2019). Interestingly, inter- and intraspecific crosses between diploids with similar karyotypes ( $2n=16$ ) resulted in the formation of diploids, triploid and tetraploid hybrids (Conceição *et al.*, 2018), indicating that diploids produce reduced and unreduced gametes.

In Plumbaginaceae, embryo sac development follows a tetrasporic pattern (Boyes and Battaglia, 1951). The few examples with embryological analysis in *Limonium* revealed that sexual diploids form reduced embryo sacs of the Gagea- type (see Maheshwari, 1937), or Adoxa- and Drusa-types (Hjelmqvist and Grazi, 1964; Róis *et al.*, 2016) (Supplementary Table 2). Triploids show diplospory of Ixeris- and Eryngium-types (*L. virgatum*, D'Amato, 1940; 1949). In facultative apomicts (diploid *L. ovalifolium*) and male-sterile species (*L. multiflorum*), Rudbeckia-type diplospory was observed (Róis *et al.*, 2016). Autonomous endosperm formation has been observed in all apomicts for which cytoembryological studies were performed (D'Amato, 1940; 1949; Hjelmqvist and Grazi, 1964; Róis *et al.*, 2016). Abiotic stress at high and low temperatures can induce changes in apomixis expression in tetraploid *L. transwallianum* (Hjelmqvist and Grazi, 1964). A *Limonium* ovule transcriptomic study revealed major pathways potentially associated with apomixis like protein degradation, transcription, stress response, hormonal signaling, signal transduction, and epigenetic regulation (Caperta *et al.*, 2023).

In conclusion, over the last years efforts have been made to uncover new information on hybridization, polyploidy and apomixis in *Limonium*. However, there are several issues which remain to be addressed like the determination and frequency of allo- vs. autopolyploid origins of extant apomictic genotypes, or competitive and reproductive interactions between species.

### C. Rosaceae

Rosaceae is one of the trio of families cited for the great frequency with which genera exhibit gametophytic apomixis (Asker and Jerling, 1992). Within the Rosales, Rosaceae are basal to the other eight families in the order, three of which also show some form of apomixis, albeit at much lower frequencies (Hojsgaard *et al.*, 2014a). The family is now recognized (Potter *et al.*, 2007; Stevens, 2001 onwards) as comprising three subfamilies and 15 tribes, eight of which include genera now well known for the taxonomic complexity

following from the combination of gametophytic apomixis, hybridization, and polyploidy. One of these subfamilies, Amygdaloideae, is a diverse group including not only many genera with dry, dehiscent fruits but also quite a few with fleshy fruits. Among these, tribe Maleae stands out because it appears to have arisen through a whole-genome duplication possibly associated with hybridization, at least 50 million years ago (Evans and Campbell, 2002; Velasco *et al.*, 2010; Hodel *et al.*, 2021). Within this tribe, most genera are fleshy-fruited (subtribe Malinae; fleshy fruits developing from hypanthial (inferior) ovaries) and many of these comprise apomictic polyploids as well as diploids. One genus, *Crataegus* L. (hawthorn), will be used to exemplify current areas of research related to apomixis, and the issues that they address.

### 1. *Crataegus*

Hawthorns, together with apples (*Malus*), cotoneasters (*Cotoneaster*), mountain ashes (*Sorbus sensu lato*), and serviceberries (*Amelanchier*), are large genera in subtribe Malinae. Gametophytic apomixis, polyploidy, and hybridization all appear to have contributed to their large numbers of species and taxonomic complexity (Dickinson *et al.*, 2007). Hawthorns differ from these genera, and from most other Malinae, in producing drupes rather than berries. *Crataegus* is estimated to comprise over 200 species native to North America, Eurasia, and North Africa (Phipps, 2015). These species are sufficiently diverse morphologically that there has been a well-developed infrageneric classification of the genus to sections or series or both since the first half of the 19<sup>th</sup> century (summarized by Phipps, 1983a; Phipps, 1983b). Hybridization was controversial, and some early 20th century North American workers pointed to the uniformity of batches of seedlings as proof that their parent tree could not be a hybrid (Dickinson, 1999), notwithstanding work in Europe documenting morphologically intermediate hawthorns and their putative parent species (Raunkjær, 1925). Polyploidy was documented in *Crataegus* around the same time, leading some workers to infer from patterns of morphological variation that apomixis also occurred in *Crataegus* (Dickinson, 1999; Talent and Dickinson, 2005).

In fact, apomixis in *Crataegus* was not demonstrated embryologically until a series of papers by Muniyamma and Phipps (1979a; 1984a; 1984b; 1985), followed by one from Ptak (1989), and more from Phipps' students (Dickinson and Phipps, 1986; Smith and Phipps, 1988; Dickinson *et al.*, 1996). The occurrence of apomixis in some *Crataegus* species studied,

and the contrast with a sexual species, was correlated with the degree of morphological variability in samples of local populations (topodemes; Dickinson and Phipps, 1985; Dickinson, 1986; Dickinson and Campbell, 1991). Subsequently, microsatellite data were used to demonstrate a parallel contrast in genetic variability in seed families in two of the same species (greater genetic variation in seed families of the sexual diploid shown to be morphologically more variable, compared to the apomictic tetraploid; Lo *et al.*, 2010b). Both of these results have implications for interpreting *Crataegus* species defined only by constant small differences in morphology.

Flow cytometry has become commonplace, and its use in estimating not only ploidy level (Dickson *et al.*, 1992; Talent and Dickinson, 2005) but also breeding system (Matzk *et al.*, 2000; FCSS) have revolutionized these aspects of comparative biology. These flow cytometric data have provided insights into whether and how apomictic seed develop, notably in response to, or independently of, the balance between maternal and paternal contributions to the endosperm (see below regarding pseudogamy; Talent and Dickinson, 2007a; Talent and Dickinson, 2007b; Talent and Dickinson, 2007c; Talent, 2009; Vašková and Kolarčík, 2019; Kolarčík *et al.*, 2022; see also *Boechea*, below). In the case of Rosaceae apomicts, this is a crucial point, since seed set in triploids and pentaploids, whether fertilized by their own pollen or the reduced pollen of diploids or tetraploids, depends on relaxation of a requirement for a 2:1 ratio of maternal to paternal genomes in their endosperm (Talent, 2009; Kolarčík *et al.*, 2022). Not only that, it has become clear that fertilization of the unreduced female gametes in individuals with gametophytic apomixis is probably the major route to polyploidization (Harlan and de Wet, 1975; Lewis, 1980; Talent and Dickinson, 2007c). Ready access to data on ploidy level variation also enables workers to prioritize analyses of diploids in molecular phylogenetic studies, and to successfully interpret results, for example, where polyploids are included in phylogenies (see below).

Insights from flow cytometry, like those from embryology, by themselves say little about the conditions under which seeds are produced. Controlled pollinations round out the picture by showing whether, and whose, pollination is needed for seed set to occur. Experiments by Bradshaw (1971), Love and Feigen (1978), and others (Dickinson and Phipps, 1986; Smith and Phipps, 1988; Wells and Phipps, 1989; Dickinson *et al.*, 1996; Talent and Dickinson, 2007c; Vašková and Kolarčík, 2019) have shown that diploid, but not polyploid, *Crataegus* are self-incompatible.

This accords with observations that gametophytic self-incompatibility prevails in the Rosaceae (Igc and Kohn, 2001), and may break down in polyploids (Lewis, 1947; Hauck *et al.*, 2006). These pollination experiments have also demonstrated that apomixis in *Crataegus* is pseudogamous, that is, endosperm fertilization by one or both sperm nuclei is required for successful seed set (Dickinson *et al.*, 1996; Dickinson *et al.*, 2007; Talent and Dickinson, 2007c; Vašková and Kolarčík, 2019; Kolarčík *et al.*, 2022). These experiments have also demonstrated that in *Crataegus* any endosperm balance requirement is relaxed, enhancing seed set in triploids. Noirot *et al.*, (1997) have pointed out that in hermaphroditic pseudogamous apomicts like *Crataegus* the evolutionarily stable strategy requires self-compatibility in such a way that male function increases with the rate of self-pollination. In *Crataegus* flowers, female function is limited to one to five locules per flower, each containing two superposed ovules of which only the lowermost has its micropyle adjacent to the funicular obturator and so is likely to be fertilized (Dickinson and Phipps, 1986; Celotti, 1995). In this way *Crataegus* approaches the situation found in grasses (a single ovule per flower) for which Noirot *et al.* (1997) developed a model predicting continued allocation to male function in pseudogamous apomicts, on the basis that self-compatibility will not be associated with inbreeding depression because the embryo develops parthenogenetically. Instead, self-compatibility contributes to fecundity (Dickinson *et al.*, 2007). And, contrary to predictions made by Cruden (1977), pollen production in *Crataegus* flowers is high regardless of ploidy level and breeding system (pollen fertility varies; Dickinson *et al.*, 1996; Dickinson and Phipps, 1986). As Charnov (1982) points out (without regard to apomixis), pollen serves not to ensure seed set, “but as an equivalent (to seeds) means toward fitness gain.”

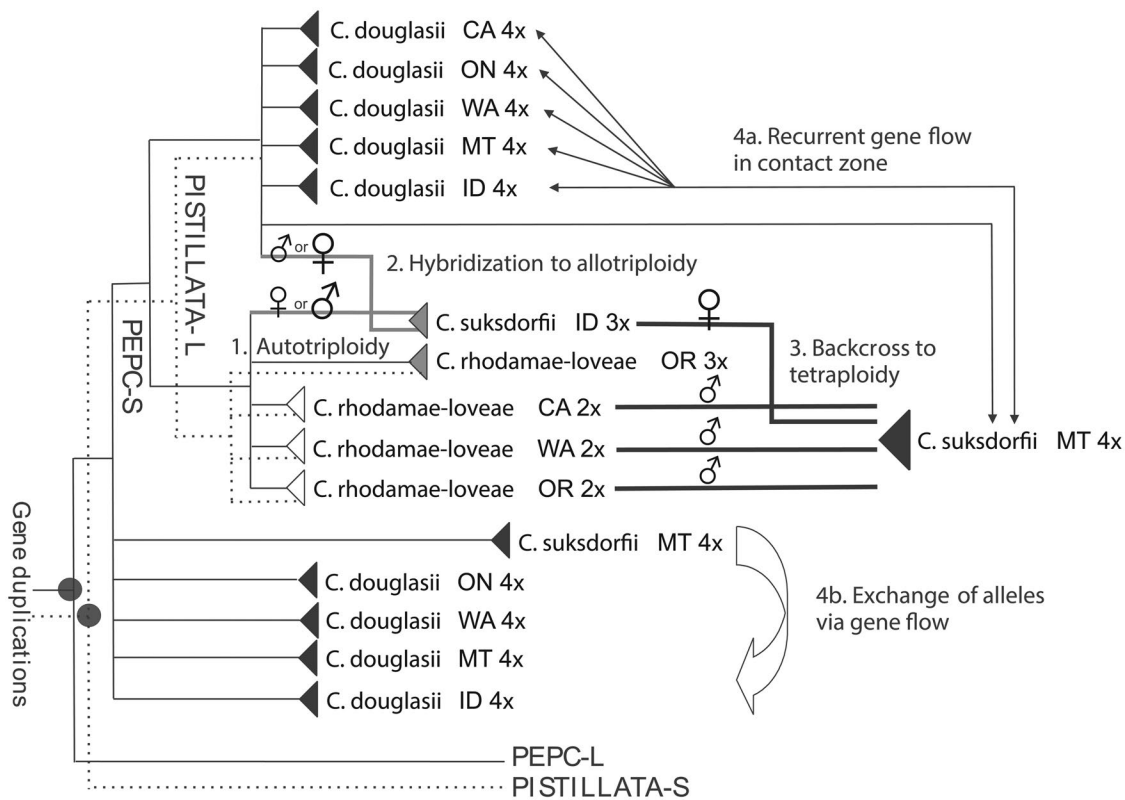
Mid-20th century floristic and taxonomic treatments increasingly admitted that some taxa might be best interpreted as hybrids (e.g. Bradshaw, 1953; Bradshaw, 1971; Byatt, 1975; Phipps, 1984; Christensen, 1992). Detailed studies involving confirmatory pollination experiments have been made (Bradshaw, 1971; Love and Feigen, 1978; Wells and Phipps, 1989), as well as studies of flowering phenology looking for opportunities for pollen exchange between species (Figure 1 in Campbell *et al.*, 1991; Kuhn and Ruprecht, 2022). Nevertheless, some (of the same) authors have deprecated the frequency and significance of hybridization (Phipps, 2005; Haines, 2011). Unrecognized hybridization together with, in any case, scant cladistically relevant morphological variation, undoubtedly contributed

to the limited success of early applications of cladistic methods to *Crataegus* problems (Phipps, 1983b; Phipps, 1984; Phipps, 1999; Dickinson and Love, 1997).

The opportunity to obtain DNA barcode sequences from the Canadian Center of DNA Barcoding at Guelph, Ontario, and to contribute to the Center’s Canadian DNA barcoding initiative, produced data from ITS2 and four plastid loci for a relatively large sample of mainly North American *Crataegus* taxa (Zarrei *et al.*, 2014; Zarrei *et al.*, 2015; Kuzmina *et al.*, 2017). Except in the case of some diploid species, and well-known diploid×diploid hybrids (cf. Christensen *et al.*, 2014), these data were disappointingly difficult to interpret (Zarrei *et al.*, 2015). With just four plastid loci this was due to the limited sequence variability seen in Rosaceae with these loci (Potter *et al.*, 2007) and in the Maleae in particular (Campbell *et al.*, 2007). Direct sequencing of ITS2 as a barcode locus in *Crataegus*, however, was thought to have led to randomly amplifying just one of the ribotypes present in an individual. In the case of individuals proving to be allopolyploids, this completely impaired the objective of unambiguous species identification (Hollingsworth *et al.*, 2011; Zarrei *et al.*, 2015). Instead, recognition of this possible scenario led to cloning and sequencing individual ribotypes, more than one in diploids, and proportionally more in polyploids. This in turn corroborated the model of hawthorn polyploidization proposed by Lo (Figure 3; Lo, 2008; Figure 5 in Lo *et al.*, 2010a), and led to discovering the probable parentage of several apomictic allopolyploid hawthorn taxa in the sample (Figure 5 in Zarrei *et al.*, 2014).

Besides enabling comparisons of the ribotype complements of diploids and polyploids, analyses of DNA sequence data have been highly successful for relating the infrageneric classification of *Crataegus* to the phylogeny of the genus. Lo *et al.* (2007) studied 33 mostly diploid ingroup accessions (including two species then assigned to *Mespilus*), plus outgroups (*Amelanchier*, *Aronia*, *Malus*) and used nrITS and the *LEAFY* second intron, and four plastome intergenic spacers, to obtain two almost identical tree topologies. Only three species that formed a clade on the nuclear tree were dispersed across the plastid tree. Subsequent work using the same and additional accessions, and increasingly larger samples of the nuclear and (or) plastid genomes, have produced the same overall topology, while adding critical species to these trees that map so well to the now updated infrageneric classification (Lo *et al.*, 2009b; Lo and Donoghue, 2012; Ufimov and Dickinson, 2020; Ufimov *et al.*, 2021; Liston *et al.*, 2021; Wu *et al.*, 2022; Figure 1 in Zarrei *et al.*, 2015).





**Figure 3.** A summary model based on the results of sequence and flow cytometry data (Lo *et al.*, 2010b), indicating parental lineages and gene flow in the diploid–polyploid complex of *Crataegus suksdorfii* sensu lato and *C. douglasii*. Solid lines indicate topologies resulting from *PEPC* data whereas dotted lines indicate *PISTILLATA* data. Four routes for polyploid formation are inferred (see Results and Discussion in Lo *et al.*, 2010b for details): (1) Autopolyploids have apparently arisen through fertilization of unreduced female gametes in diploids (Considine *et al.*, 2012) and have persisted in colder habitats (Lo *et al.*, 2013; McGoey *et al.*, 2014); note that autotriploids treated elsewhere as *C. gaylussacia* (Dickinson *et al.*, 2021; Dickinson and Han, 2023) were not sampled by Lo *et al.* (2010b). (2) Branches in gray indicate hybridization between 2x *C. suksdorfii* sensu lato (now named *C. rhodamae-loveae*; Dickinson & Han 2023) and 4x *C. douglasii*. (3) Bolded branches indicate the backcrossing of the allotriploids with their diploid progenitors. (4) Lines with arrows indicate recurrent gene flow between the sympatric 4x *C. suksdorfii* sensu stricto and 4x *C. douglasii*. This figure is reproduced from Lo (2008) with permission of the author and corresponds (with a minor correction made here, to Figure 5 in Lo *et al.*, 2010b).

Hawthorn biogeography has been studied not only in relation to phylogeny (e.g. Lo *et al.*, 2009b; Ufimov and Dickinson, 2020) but also with respect to the impact of apomixis on geographic distributions (geographic parthenogenesis; Hörandl, 2006). Surveying *Crataegus* in Ontario, Canada, an area totally covered by glacial ice until 13,000 years ago, most of the 20 native species studied are either triploid or tetraploid, and only four are diploid (Muniyamma and Phipps, 1979b). A species complex like *C. crus-galli*, widely distributed in southern Ontario (and eastern North America generally) is exclusively apomictic and tetraploid there, but turns out to have diploids in Alabama and Georgia (Dickinson and Phipps, 1986; Talent and Dickinson, 2005; Talent and Dickinson, 2007b). The more sparse *Crataegus* flora of western North America includes a native diploid species, *C. rhodamae-loveae* that is restricted to a largely

unglaciated area in Oregon west of the Cascades Range, and adjacent portions of California and Washington (Dickinson and Han, 2023). Apomictic allopolyploid *Crataegus* species shown to be related to *C. rhodamae-loveae* (all in *C. sect. Douglasianae*) have much wider distributions, two of them (*C. douglasii* and *C. suksdorfii*) extending not only well north of the glacial maximum but also to the east (*C. douglasii*), with a disjunct presence in the previously glaciated upper Great Lakes basin (Dickinson *et al.*, 2021). The contrasting distributions of the diploid and allopolyploid species have been characterized with respect to climate parameters in a series of papers that show the diploids (and closely related autotriploids) restricted to relatively warmer and more mesic habitats than the allopolyploids (Lo *et al.*, 2009a; Lo *et al.*, 2013; McGoey *et al.*, 2014; Coughlan *et al.*, 2017; Dickinson *et al.*, 2021).

A second western diploid, *Crataegus saligna* (C. sect. *Salignae*), is the only species studied that exhibits a morphological feature (denser second and higher order leaf venation) that could be interpreted as possibly adaptive in more xeric habitats (Dickinson *et al.*, 2021). Two closely related apomictic allopolyploid species (also C. sect. *Salignae*; similarly, *C. douglasii* and *C. suksdorfii*) lack this feature, but have wider geographic distributions (Dickinson *et al.*, 2021).

Coughlan *et al.* (2014) examined relative biomass allocations to fruit components (mesocarp, endocarp, seed) in diploids, autotriploids, and allopolyploids and interpreted the results as showing greater allocation to establishment (seed mass) in diploids and autotriploids, in contrast to greater allocation to dispersal (fruit mass) in the allopolyploids. Features promoting dispersal and differentiating allopolyploids from diploids and autotriploids include not only polyploid self-compatibility but also greater environmental amplitude, greater allocation to dispersal, morphological features (stamen number per flower), and (in the *Salignae*) leaf venation density, all of which are attributable to hybridization with the putative other (non-*Douglasianae*, non-*Salignae*) parent of the allopolyploids (Coughlan *et al.*, 2017; Dickinson *et al.*, 2021; Liston *et al.*, 2021). In terms of climatic niches, only the autotriploids are markedly differentiated. The other taxa and ploidy levels studied in these western North American hawthorns are not greatly differentiated ecologically, and diploids occupy subsets of the allopolyploid climate spaces. The most nearly comparable study of European hawthorns (Kuhn and Ruprecht, 2023) is much more local in scale, and analyzes a wider range of habitat variables (climate, landscape, microenvironment) in order to contrast hybrids and their parent species without reference to breeding system.

#### D. Brassicaceae

The Brassicaceae (mustard family, crucifers) is a globally distributed family, comprising 3,977 species across 351 genera (German *et al.*, 2023). It originated between the late Eocene and late Oligocene and split into two subfamilies (Aethionemoideae and Brassicoideae), with five supertribes in the latter (Arabodae, Brassicodae, Camelinodae, Heliophilodae, and Hesperodae), and a total of 58 tribes (BrassiToL: <https://brassitol.vercel.app/>, Hendriks *et al.*, 2023). The Brassicaceae is important both scientifically and economically, housing the iconic model plant *Arabidopsis thaliana* and crops that feed billions of people worldwide.

Apomixis is relatively uncommon in the family Brassicaceae, primarily occurring in the tribe Boechereae, which currently includes nine genera (Mandáková *et al.*, 2020; Hay *et al.*, 2023). Seven of these (*Anelsonia*, *Cusickiella*, *Nevada*, *Phoenicaulis*, *Polycytenium*, *Sandbergia*, and *Yosemitea*) are mono- or bispecific and are confined to the western United States. The genus *Borodinia* includes eight species (Alexander *et al.*, 2013); seven of these are restricted to eastern North America and one is endemic to Siberia and coastal northeast Asia. *Boechera*, with more than 480 genetically distinct taxa (Li *et al.*, 2017), is the most widespread genus in the tribe, distributed southward from Alaska through most of North America and extending to Greenland (1 species) and another to Siberia (1 species) (Alexander *et al.*, 2013). All Boechereae genera and intrageneric *Boechera* clades are well defined, and a backbone phylogeny for tribe-wide evolutionary inference is available (Hay *et al.*, 2023).

The Boechereae appear to be a “hotspot” for the origin and diversification of apomictic taxa. Gametophytic apomixis has been documented or inferred in over 100 *Boechera* taxa, substantially augmenting genotype and phenotype diversity by stabilizing the outcomes of reticulate evolution (Carman *et al.*, 2019). Embryological investigations have revealed the occurrence of three distinct types of gametophytic apomixis in both diploid and triploid *Boechera* taxa: Antennaria-type diplospory, Taraxacum-type diplospory, and Hieracium-type apospory (Windham *et al.*, 2016; Carman *et al.*, 2019). The occurrence of the Antennaria-type in *Boechera* is rare, primarily observed in plants otherwise reproducing through Taraxacum-type diplospory. In contrast, Taraxacum-type diplospory and apospory are more prevalent in natural *Boechera* populations than sexual reproduction. Plants expressing apospory and diplospory are equally common, and in seven *Boechera* taxa, simultaneous occurrence of apospory and diplospory was uncovered, each at elevated frequencies (Carman *et al.*, 2019). Furthermore, apospory has been embryologically documented in four additional genera within the Boechereae: diploid *Borodinia laevigata* (Carman *et al.*, 2019), di-, tri- and tetraploid *Phoenicaulis cheiranthoides* (Mandáková *et al.*, 2021), tetraploid *Polycytenium fremontii* (Mandáková *et al.*, 2020), and triploid *Sandbergia whitedii* (Mandáková *et al.*, 2020).

#### 1. *Boechera*

The genus *Boechera* exhibits a basic chromosome number  $x=7$ , with sexual species being diploid

( $2n = 14$ ). Although primarily autogamous (self-pollinating), natural occurrences of interspecific hybrids (allodiploids;  $2n = 14, 15$ ) involving sexual *Boechera* diploids are frequent (Kantama *et al.*, 2007; Beck *et al.*, 2012; Aliyu *et al.*, 2013; Alexander *et al.*, 2015; Mandáková *et al.*, 2015; Li *et al.*, 2017; Mandáková *et al.*, 2020). These hybrids typically exhibit apomixis, which represents an escape from the (semi)sterility otherwise characteristic of allodiploid hybrids, facilitating their persistence within populations. Although prevalent in *Boechera*, the emergence of apomixis in allodiploid hybrids formed between two sexual diploid species is rare among other angiosperms (Carman, 1997). In this respect, many apomictic *Boechera* also produce unreduced ( $2n$ ) pollen, a feature generally rare among other angiospermous apomicts (Asker and Jerling, 1992). In *Boechera*,  $2n$  sperm from apomictic diploids can fertilize  $1n$  eggs of co-occurring sexual taxa, giving rise to novel and genomically unique triploid apomicts ( $2n = 21, 22$ ) (Böcher, 1951; Alexander *et al.*, 2015; Li *et al.*, 2017; Mau *et al.*, 2021). Apomictic *Boechera* tetraploids also arise through this mechanism, albeit significantly less frequently (Schranz *et al.*, 2005; Aliyu *et al.*, 2010). Apomictic hybrids demonstrate somewhat broader ecological competencies compared to the sexual progenitors (Windham and Al-Shehbaz, 2006; Alexander *et al.*, 2015; Windham *et al.*, 2016; Shah *et al.*, 2016; Rushworth *et al.*, 2018), but the major driver of niche divergence appears to be ploidy level (Mau *et al.*, 2015).

The genome structure was reconstructed in Boechereae species across seven genera: *Boechera*, *Borodinia*, *Cusickiella*, *Phoenicaulis*, *Polycytenium*, *Nevada*, and *Sandbergia* (Mandáková *et al.*, 2015; Lee *et al.*, 2017; Mandáková *et al.*, 2020; Mandáková *et al.*, 2021). All analyzed taxa shared a common seven-chromosome genome structure ( $x = 7$ ). Comparative analysis with the sister tribe Halimolobeae ( $x = 8$ ) indicated that the ancestral Boechereae genome ( $n = 7$ ) originated from an older  $n = 8$  genome through descending dysploidy, followed by the divergence of extant Boechereae taxa approximately eight million years ago (Mandáková *et al.*, 2020). While three chromosomes (Boe4, 6, 7) retained their ancestral structure, five chromosomes underwent reshuffling via end-to-end translocation, two reciprocal translocations, and a pericentric inversion, resulting in the formation of chromosomes Boe1-3 and Boe5 (Mandáková *et al.*, 2015; 2020). Despite the general genomic conservatism observed in most Boechereae genera, intra-tribal cladogenesis has occasionally been associated with chromosome rearrangements, particularly inversions (Mandáková *et al.*, 2020). Notably,

a recent large pericentric inversion has been identified in *Boechera stricta* which controls ecologically important traits distinguishing populations (Lee *et al.*, 2017). This suggests that such chromosome rearrangements may play a crucial role in reproductive isolation during incipient speciation.

Because of its small genome (~250 Mb), close evolutionary relationship to *A. thaliana* (Song and Mitchell-Olds, 2007; Hendriks *et al.*, 2023), and naturally occurring diploid sexual and diploid apomictic lines, the genus *Boechera* has become a subject of intense research interest. The existence of diploid apomictic lines shows that polyploidy is not a requirement for the expression of apomixis. Genomic in situ hybridization demonstrated that the *Boechera* apomicts are interspecific hybrids with variable numbers of parental chromosomes (Kantama *et al.*, 2007). This variation is caused by the substitution of homeologous parental chromosomes in apomictic hybrids. A second peculiarity is the presence of heterochromatic supernumerary chromosomes in apomictic genomes. Apomictic *Boechera* plants with 15 chromosomes were described as early as in 1951 (Böcher, 1951). Later studies described the supernumerary B-like chromosomes in aneuploid apomicts ( $2n = 2x + 1 = 15$ ,  $2n = 3x + 1 = 22$ ) as being heterochromatic and often smaller than the other chromosomes (Sharbel *et al.*, 2004; Sharbel *et al.*, 2005). As these chromosomes were absent in sexual diploids and present in apomictic diploid ( $2n = 15$ ) and triploid ( $2n = 22$ ) lines, it was argued that B-like chromosomes may contain genetic elements associated with the apomictic trait (Sharbel *et al.*, 2004; Sharbel *et al.*, 2005). Comparative analyses of the mitotic and meiotic chromosomes of sexual and apomictic lines demonstrated that all diploid apomicts have one highly heterochromatic (Het) chromosome. An additional smaller chromosome, referred to as Del (“deletion chromosome”), was found in diploid and triploid apomictic aneuploids (Kantama *et al.*, 2007). Later cytogenetic screening of diploid apomicts revealed that the Het chromosome in 14-chromosomal apomicts is one of the Boe1 homeologs, which encompasses genomic blocks A1, C1, and D, and exhibits expanded pericentromeric heterochromatin (Mandáková *et al.*, 2015). In aneuploid apomicts ( $2n = 15$ ), telocentric Het' (blocks A1 and C1) and Del (block D) chromosomes originated through breakage within the heterochromatin/repeat-rich Het centromere (centric fission) (Mandáková *et al.*, 2015). The stable inheritance of the heterochromatic fission chromosomes is probably due to the apomictic mode of reproduction. Notably, centric fission in *Boechera*

is the only example of this rearrangement (and ascending dysploidy) in the family Brassicaceae. Furthermore, the chromosome localization of the apomixis-associated factor UPGRADE2 on Boe1 hom(e)ologs showed a significant increase in copy number on Het and Het' in  $2n=14$  and  $2n=15$  apomicts, respectively (Mau *et al.*, 2022). This finding indicates a possible functional link between the expansion of pericentromeric heterochromatin on Het and Het' chromosomes and the amplification of UPGRADE2 gene copy number. The consistent presence of the UPGRADE2-bearing Het chromosomes in all apomictic lineages suggests its key role in controlling the apomictic trait.

## 2. *Draba*

*Draba* (Arabideae), is the most diverse genus in the family Brassicaceae, comprising over 420 species distributed across the Northern Hemisphere and Andean South America. Currently, 13 species of *Draba* have been proposed to exhibit apomixis: *D. aretioides* (Ptáček *et al.*, 2024), *D. crassa* (Price, 1979; Decker, 2006), *D. densifolia* (Mulligan, 1976; Mulligan, 2021), *D. exunguiculata* (Price, 1979; Price and Rollins, 1991), *D. globosa* (Windham *et al.*, 2023), *D. grayana* (Price, 1979; Price and Rollins, 1991), *D. novolympica* (Mulligan, 1971; Mulligan, 2021), *D. oligosperma* (Mulligan and Findlay, 1970; Mulligan, 1972), *D. streptobrachia* (Price, 1979; Price, 1980), *D. taylori* (Al-Shehbaz and Mulligan, 2013; Mulligan, 2021), *D. trichocarpa* (Al-Shehbaz *et al.*, 2010), *D. ventosa* (Mulligan, 1971), and *D. weberi* (Price and Rollins, 1991; Decker, 2006). These species, except for *D. aretioides*, are deduced to produce seeds through apomixis, consistently yielding viable seeds despite disruptions in male meiosis, leading to indehiscent anthers and/or limited viable pollen. Autonomous apomixis was confirmed in *Draba oligosperma* via emasculation experiments (Mulligan, 1972). These twelve species are indigenous to the mountainous regions of western North America and demonstrate diverse levels of evolutionary success. Species like *D. trichocarpa* and *D. weberi* are very rare, each known from a single small population. Conversely, species such as *D. densifolia*, *D. novolympica*, *D. oligosperma*, and *D. ventosa* are widely distributed across western United States and Canada. While the ploidy levels of three of the twelve species remain undetermined, the remaining nine are all polyploid. The most recent addition to the list of putative apomictic *Draba* species is *D. aretioides*. Apomixis was suggested in this species based on

FCSS (Ptáček *et al.*, 2024) and requires further support. Notably, *D. aretioides* differs from the previously discussed taxa in its geographic distribution (Andean South America).

## 3. *Cardamine*

The genus *Cardamine* (Cardamineae), encompassing approx. 200 species (Carlsen *et al.*, 2009), is widely distributed in temperate climates and occasionally exhibits weedy behavior. Embryological studies by Ančev *et al.*, (2013) have revealed that the Bulgarian triploid hybrid *C. ×rhodopaea* is capable of agamospermy through Taraxacum-type meiotic diplospory. Another potential occurrence of apomixis in *Cardamine* was observed in the Swiss triploid hybrid *C. ×insueta*. Although Urbanska *et al.*, (1997) initially suggested polarized meiosis as the likely mechanism for seed production in this taxon, subsequent studies by Mandáková *et al.* (2013) emphasized the critical role of unreduced (diplosporous) embryo sac production in the evolutionary trajectory of the species complex. Other genera within the Cardamineae tribe showing reproductive/genetic anomalies suggestive of apomixis include *Rorippa* (Bleeker and Matthies, 2005), *Nasturtium* (Bleeker *et al.*, 1999), and *Leavenworthia* (Edwards *et al.*, 2022).

## 4. *Iberis*

In the small genus *Iberis* (approx. 25 species, Iberideae), embryological investigations of triploid Bulgarian populations of *I. saxatilis* have documented the production of viable seeds through diplospory and apospory (Yurukova-Grancharova *et al.*, 2004).

## 5. *Brassica: a case of inducible apomixis*

In *Brassica* (Brassicaceae), which encompasses most major Brassicaceae crops, cytological studies have identified developmental pathways in artificial crosses resembling those of known apomicts. For instance, Praekelt and Scott (2001) observed that artificial crosses between diploid *B. oleracea* and various other species exhibited two critical components of apomixis: the presence of unreduced embryo sacs and the inherent ability for parthenogenesis. This phenomenon appears to be more pronounced in crosses between phylogenetically distant species, contributing to reports of agamospermy in artificial hybrids between *B. napus* and *Raphanus sativus* (Dobeš *et al.*, 2007; Ellerström, 2008; Ellerström and Zagorcheva, 2009). Evidence for apomixis in natural populations, however, is so far missing.



## 6. Genera with doubtful records

*Erysimum* (Erysimeae) stands as the second most diverse genus in the mustard family, boasting approximately 220 species primarily concentrated in Eurasia (Al-Shehbaz, 2012). Similar to the majority of *Draba* species discussed above, the presence of apomixis in *Erysimum* has been suspected from observations of abundant seed production in plants that yield little to no viable pollen. *Erysimum inconspicuum* is a widely distributed native species extensively studied by Mulligan (1966), who identified two distinct ploidy levels in the species. Another species, tentatively identified as *E. hieracifolium*, was hypothesized to be apomictic by Mulligan and Frankton (1967) due to irregular pollen meiosis, but this can also occur in sexual polyploids. Further evidence of apomixis is missing. This taxon, known for its aggressive weediness in eastern Canada, exhibits notable differences from typical European populations of *E. hieracifolium* s.s., including variations in ploidy level. It is speculated that this taxon may have originated in situ through interactions between species that were geographically isolated prior to European colonization.

*Parrya* (Chorispora) comprises approximately 40 species found across mountainous regions in central Asia, arctic Eurasia, and northern North America (Al-Shehbaz and German, 2013). In a study by Mosquin and Hayley (1966), diploid ( $2n=14$ ) and triploid ( $2n \approx 21$ ) individuals of *P. arctica* were encountered. They suggested a close morphological connection between *Parrya* and *Boechnera*, noting their shared chromosome base number ( $x=7$ ). They proposed that *P. arctica*, similar to *Boechnera*, may exhibit facultative apomixis (Mosquin and Hayley, 1966). However, the authors did not provide standard information on meiotic irregularities, pollen viability, or abundant seed production to support this inference of agamospermy, despite the presumed impairment of microsporogenesis in the triploid individual. Furthermore, recent molecular phylogenetic analyses did not confirm the close relationship between *Parrya* and *Boechnera* (Hendriks et al., 2023). Although *P. arctica* has often been cited as an established example of apomixis (Schmidt, 2020), considering the aforementioned circumstances, it has been excluded from our compilation of well-documented cases of apomixis in the Brassicaceae.

We have also excluded a recent report of apomixis in *Mancoa* from our list. This genus, comprising eight species assigned to tribe Halimolobeae, is found in northern Mexico and Andean South America (Bailey et al., 2007). Ptáček et al., (2024) reported autonomous

apomixis in a Bolivian sample of *M. hispida*, based on FCSS only. However, *M. hispida* is an annual species, and apomictic annuals are exceptionally rare (Hörandl, 2010). If further confirmed through embryological investigation, this finding would be significant due to the rarity of apomixis in both annual plants and non-North American mustard species. Moreover, the fact that *M. hispida* belongs to Halimolobeae, a sister tribe to the extensively apomictic Boechnereae (Hay et al., 2023; Hendriks et al., 2023), makes this case even more interesting for further research.

In summary, apomixis is relatively uncommon but phylogenetically dispersed in Brassicaceae. Apomixis is most prevalent in the genus *Boechnera* where it arises through both homoploid hybridization in diploids and unreduced gamete formation leading to allopolyploidy or autopolyploidy (Carman et al., 2019). Extensive reticulate evolution and stabilization of hybrids via apomixis makes *Boechnera* taxonomy very complex (Li et al., 2017). While the majority of apomictic species in the group are endemic to western North America, this pattern may potentially diminish with additional sampling efforts. Most reports published to date infer the presence of apomixis through indirect evidence, such as the development of viable seeds in the absence of typical, meiotically-produced pollen. Future studies employing embryological techniques are anticipated to provide direct insights into the apomixis process.

## E. Rutaceae

Rutaceae consist of about 2,100 species in 154 genera and is mainly distributed in tropical and sub-tropical regions worldwide (Appelhans et al., 2021). The family is best known for the economically important *Citrus* species, hybrids and cultivars. Apomixis has been reported for several genera of Rutaceae, but it has only been studied in detail in *Citrus* (s.l., including *Fortunella* and *Poncirus*) and few *Zanthoxylum* (incl. *Toddalia*) species. Typically, apomictic Rutaceae reproduce via adventitious embryony and seeds are often polyembryonic (Naumova, 1993; Hojsgaard and Pullaiah, 2023). In two genera, *Skimmia* and *Triphasia*, apospory has been identified as the apomictic pathway (Desai, 1961; Hojsgaard and Pullaiah, 2023). Reports on apomixis of Rutaceae genera are often not based on the study of embryo sac development and/or flow cytometry, but instead on the occurrence of polyembryony. Genera for which polyembryony has been reported include *Aegle*, *Atalantia*, *Citrus*, *Conchocarpus* (incl. *Almeidea*), *Esenbeckia*, *Feroniella*, *Haplophyllum*

[as *Ruta*], *Murraya*, *Ptelea*, *Triphasia*, and *Zanthoxylum* (Mauritzon, 1935; Webber, 1940; Hossain *et al.*, 1993; Carman, 1997; Kubitzki *et al.*, 2011; Hojsgaard and Pullaiah, 2023). Up to 40 embryos have been observed in a single *Citrus* seed, but normally only up to three develop (Ueno *et al.*, 1969; Kubitzki *et al.*, 2011). The occurrence of polyembryony does not necessarily mean that the taxon reproduces apomictically, since the polyembryonic condition could be due to more than one megasporocyte developing into an embryo sac, differentiation of an antipodal or synergid cell into an additional egg cell, or cleavage embryony, in which a zygote or young embryo separates into two or more units (Webber, 1940; Hojsgaard and Pullaiah, 2023). However, as far as it is known, the additional embryos in all polyembryonic Rutaceae develop from nucellar tissue (Mauritzon, 1935; Bai and Lakshmanan, 1982; Naumova, 1993).

In addition to the above-mentioned genera, apomixis has been proposed for *Glycosmis pentaphylla* because of the occurrence of ortho- and anorthopolyploidy in this species complex (i.e. even or odd number of chromosome sets, respectively; Guerra, 1980; Samuel *et al.*, 2001). Diploid, pentaploid and hexaploid cytotypes have been documented for this species (Samuel *et al.*, 2001; Mou and Zhang, 2012).

In total, apomixis has been reported from 13 out of 154 genera in the family. Seven of these belong to the *Citrus* subfamily Aurantioideae, which contains 27 or 28 genera in total (Appelhans *et al.*, 2021) and one belongs to the monogeneric Haplophylloideae. The remaining five genera are part of the largest subfamily Zanthoxyloideae and are not closely related (Appelhans *et al.*, 2021; Joyce *et al.*, 2023).

### 1. *Citrus*

*Citrus* ranks among the economically most important crop genera in the world. *Citrus* is cultivated throughout the sub-tropical and tropical regions worldwide, and the natural distribution of the genus ranges from eastern and southern Asia to New Guinea, Australia and the southwest Pacific Islands (Kubitzki *et al.*, 2011; Mabberley, 2022). There has been much debate about the number of species in the genus, which varies from six to 157, depending on the author (Engler 1896; Tanaka, 1961). Currently, about 25 species are accepted for the genus (Mabberley, 2022). Apomixis in *Citrus* is known from several species, hybrids, and cultivars and has been observed in the three parental species (*C. maxima* [pomelo], *C. medica* L. [citron], *C. reticulata* [mandarin]), from which all commercially important

hybrids are derived. The circumscription of the genus has been broadened as a consequence of molecular phylogenetic analyses (Bayer *et al.*, 2009), and the former genera *Fortunella* and *Poncirus*, that also contain apomictic species, are now treated as *Citrus* (Mabberley, 2022; Hojsgaard and Pullaiah, 2023). As typical for Rutaceae, the apomictic pathway in *Citrus* is adventitious embryony with often polyembryonic seeds (Naumova, 1993; Xu *et al.*, 2021). *Citrus* pollen grains are viable and endosperm formation is the result of double fertilization (Naumova, 1993; Wang *et al.*, 2022). Molecular mechanisms that lead to apomixis in *Citrus* have recently been reviewed (Xu *et al.*, 2021), and *CitRWP* has been identified as a crucial gene for adventitious embryony (Xu *et al.*, 2021; Wang *et al.*, 2022). A knockdown of the gene resulted in exclusively sexual embryos and monoembryony, while the development of adventitious embryos was suppressed (Shimada *et al.*, 2018; Wang *et al.*, 2022).

### 2. *Zanthoxylum*

With more than 220 species, *Zanthoxylum* is the largest or second largest genus in Rutaceae and it has a pantropical distribution that extends to temperate regions in Northern America and Eastern Asia (Appelhans *et al.*, 2018; Reichelt *et al.*, 2021). *Zanthoxylum* used to be subdivided into three genera: *Fagara*, *Toddalia*, and *Zanthoxylum* s.str. (Appelhans *et al.*, 2018). While all *Fagara* and *Toddalia* species have biseriate flowers, *Zanthoxylum* s.str. species have very small and uniseriate flowers with a varying number of tepals (Reynel, 2017). The merging of *Fagara* and *Toddalia* into *Zanthoxylum* is supported by molecular phylogenetic analyses, and *Zanthoxylum* s.str. is deeply nested within former *Fagara* species (Appelhans *et al.*, 2018; Reichelt *et al.*, 2021). Apomixis has so far been documented mainly for several species of *Zanthoxylum* s.str. (Liu *et al.*, 1987; Naumova, 1993; Fei *et al.*, 2021a; 2021b; 2021c), but polyembryony has been reported for *Z. asiaticum* (as *Toddalia asiatica*; Bai and Lakshmanan, 1982) and nucellar embryos have been documented for *Z. oxyphyllum* and *Z. tragodes* (as *Z. spinifex*), which belonged to *Fagara* in the past (Naumova, 1993; Hojsgaard and Pullaiah, 2023). Thus, apomixis in *Zanthoxylum* is probably not limited to the species with uniseriate flowers.

In contrast to *Citrus*, *Zanthoxylum* species are usually functionally dioecious, with female flowers possessing staminodes and male flowers that produce rudimentary carpels. Rarely, plants can be monoecious

or polygamodioecious, bearing hermaphroditic and unisexual flowers on the same inflorescence (Hartley, 1966; Reynel, 2017). For the apomictic *Z. americanum*, plants with a smaller number of hermaphroditic flowers, as well as “male” plants bearing some ripe fruits have been observed (Munter *et al.*, 2018). *Zanthoxylum acanthopodium*, a close relative of the apomictic *Z. bungeanum* and *Z. simulans* (unpublished data M. Appelhans), for which the reproductive system is unknown, is known to be strictly functionally dioecious throughout most of its distribution (E Pakistan, N India to SW China, N Myanmar and N Thailand), but populations with a disjunct distribution in northern Sumatra appear to be exclusively hermaphroditic (Hartley, 1966). Thus, a pollen donor would be required in most species in case the endosperm development required fertilization. Conclusive studies about the requirement of fertilization for endosperm development are lacking, but viable pollen grains have been identified for the apomictic *Z. americanum* Mill., *Z. bungeanum* and *Z. simulans* (Liu *et al.*, 1987; Naumova, 1993; Munter *et al.*, 2018; Fei *et al.*, 2021a). Still, in these three species the development of seeds and endosperm without fertilization has been observed (Liu *et al.*, 1987; Munter *et al.*, 2018; Fei *et al.*, 2021a). Fei *et al.*, (2021a) measured pollen germination *in vitro* and carried out a pollination experiment on *Z. bungeanum* and they recorded a low pollen germination rate, observed pollen tube formation, but no successful fertilization. These authors also studied differential gene expression and phytohormone concentrations in fruits developed from unfertilized versus fertilized flowers (Fei *et al.*, 2021a). They report that the concentration of ABA (abscisic acid) is increased in fruits developed from fertilized flowers and that key genes in the biosynthesis pathway of ABA are upregulated. Moreover, plants that had been pollinated showed an increased fruit setting rate as did plants that had been sprayed with exogenous ABA. The authors conclude that pollination has a positive effect on fruit set by influencing gene expression and production of phytohormones (mainly ABA), but endosperm production through double fertilization was not observed.

## F. Asteraceae

The cosmopolitan family Asteraceae, with more than 1,600 genera and 25,000 species, is by far the largest family of Asterales (Stevens, 2020), and the only one in this order with apomictic genera. Noyes (2007) critically evaluated the records of apomictic reproduction in the family and confirmed 22 genera with the

presence of (fully) functional apomixis. However, this number also depends on the taxonomic concept of a particular genus. For example, genus *Hieracium* in Noyes’ review included both *Hieracium* s. str. and *Pilosella* as subgenera, whereas now there is substantial evidence for a narrower generic concept (see below). Asteraceae genera with apomixis are concentrated in seven derived tribes (Astereae, Eupatorieae, Gnaphalieae, Heliantheae, Madieae, Inulae, and Lactuceae), while they are absent from the basal tribes that evolved in the Neotropics – the evolutionary cradle of the family (Noyes, 2007). In Asteraceae, autonomous apomixis is expressed as gametophytic diplospory (17 genera) or apospory (five genera), with no evidence for effective sporophytic adventitious embryony (Noyes, 2007).

Apomixis is associated with polyploidy and hybridity, which have profoundly shaped the evolutionary patterns and, consequently, the classification of apomicts within Asteraceae. In most apomictic genera, asexual representatives form a minority of recognized taxa, usually concentrated within a specific infrageneric group. However, in *Hieracium*, *Pilosella* and *Taraxacum* (all of the Lactuceae tribe), apomixis is very widespread and is by far the predominant mode of reproduction. Here we describe the phenomenon of apomixis and its evolutionary consequences in *Hieracium* and *Pilosella*.

Both genera belong to the subtribe Hieraciinae, which in the current circumscription also includes the sexually reproducing Mediterranean-Macaronesian genus *Andryala* and *Hispidella*, a monotypic annual genus endemic to the Iberian Peninsula (Kilian *et al.*, 2009). Traditionally, the genus *Pilosella* has been treated as a subgenus of *Hieracium*, but there is ample evidence, i.e. morphological, cytological, embryological, genetic, ecological and phylogenetic evidence, that both genera should be treated separately (Zahn, 1921–1923; Asker and Jerling, 1992; Mráz, 2003; Suda *et al.*, 2007; Chrtěk *et al.*, 2009; Fehrer *et al.*, 2009; Hand *et al.*, 2015).

### 1. *Hieracium* s.str.

*Hieracium* (excluding *Pilosella*) is naturally distributed in Eurasia, northwestern Africa and the Americas. The genus consists of two subgenera with contrasting reproductive modes and taxonomic diversity. While the subgenus *Chionoracium*, which is native to the Americas, consists of approximately 150 exclusively sexual diploid species, the subgenus *Hieracium* (hereafter *Hieracium*) occurs predominantly in Eurasia and represents a huge agamic complex with species numbers varying between 500 and 5,000, depending on the species concept (Zahn, 1921–1923; Beaman, 1990; Majesky *et al.*, 2017; Fehrer *et al.*, 2022).

*Hieracium* consists of ca. 30 diploid species ( $2n=18$ ) and a vast number of morphologically more or less easily distinguishable polyploids with prevailing tri- ( $2n=27$ ) and tetraploids ( $2n=36$ ), and rare pentaploids ( $2n=45$ ) (Mráz *et al.*, 2019). Diploids occur in southern mountainous regions of the European Alpine System (the Eastern and Southern Carpathians, the Balkans, the Alps, the Pyrenees) and they are often geographically and/or ecologically isolated. In contrast, polyploids are widespread across the whole of Europe, showing a typical pattern of geographical parthenogenesis. Diploids are sexual and strictly self-incompatible, although an induced selfing (mentor effect) sometimes occurs in the presence of hetero-specific pollen which can break down the strong sporophytic self-incompatibility barrier on stigmas allowing germination of own pollen (Mráz, 2003; Mráz and Paule, 2006). This mechanism might strengthen the reproductive isolation of sexuals in frequent diploid-polyploid, and rare diploid-diploid, interspecific populations, where mixed pollen loads can be common (Mráz 2003). Apomixis, either obligate or nearly obligate, was proved in all polyploids tested so far (reviewed by Mráz and Zdvorák, 2019), and therefore this mode of reproduction is expected to be present in all polyploid hawkweeds.

Apomixis in *Hieracium* is expressed as a mitotic diplospory of the Antennaria-type (Bergman, 1935). An important feature of diplospory is frequent precocious embryogenesis – a phenomenon in which embryogenesis starts before floret opening–, preventing eventual fertilization of the unreduced gamete (Bergman, 1935; Skawińska, 1963; Hand *et al.*, 2015). Pollen production, its size heterogeneity and viability vary considerably among apomictic hawkweeds. Many of them are completely pollen sterile, while others produce less pollen compared to sexual diploids and this pollen is heterogeneous in size (Chrtek, 1997; Slade and Rich, 2007; Mráz *et al.*, 2009; Chrtek *et al.*, 2020). This is mainly due to severe developmental problems in the sporogenic tissue, and partly also to irregularities in chromosome pairing during meiosis (Rosenberg, 1917; 1927; Gentcheff and Gustafsson, 1940). Residual sexuality in apomictic polyploids was suggested by Bergman (1941) and later by Hand *et al.*, (2015), who detected a small proportion of megaspore mother cells (MMCs) that underwent meiosis. The first evidence of functional facultative apomixis in the genus was published by Mráz and Zdvorák (2019). Using FCSS, they showed that approximately 0.4% of the seed progeny produced by apomictic polyploids were formed after fertilization of either reduced or unreduced embryo sacs resulting in  $B_{II}$  or  $B_{III}$  hybrids,

respectively. Despite a low frequency of facultative apomixis, given the ubiquity of polyploid hawkweeds and their large population sizes, this process could be a relevant source of new variation in the genus.

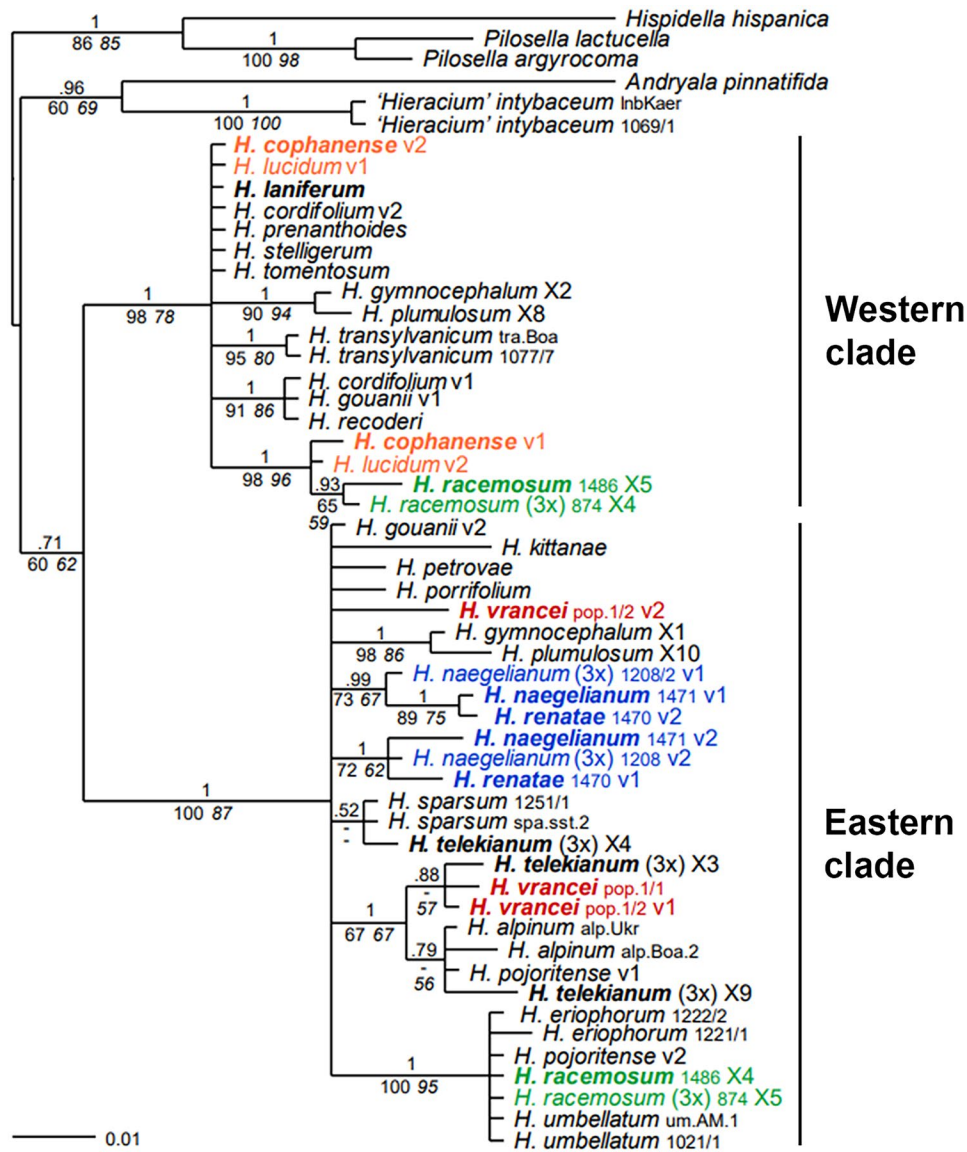
Recent interspecific hybridization between sexual diploid taxa has been confirmed in a few cases only, mostly due to their geographical or ecological separation (Mráz *et al.*, 2005; 2011; Chrtek *et al.*, 2006). Experimental crosses between sexually diploid species resulted in morphologically intermediate diploid F1 hybrids, but these were highly seed sterile likely due to problematic meiosis caused by genomic incompatibilities of parental taxa (Mráz and Paule, 2006). In this view, polyploidization closely associated with apomixis, which ensures reproduction by seeds, can provide *Hieracium* interspecific hybrids with an evolutionary perspective, or an escape from sterility in the words of Darlington (1939). Interestingly, diploid F1 hybrids produce high quantities of homogeneous-sized pollen, suggesting greater importance of F1 hybrids as putative pollen donors (Mráz and Paule, 2006; Chrtek *et al.*, 2020). In contrast to the currently rare natural interspecific hybridization, patterns of morphological and molecular variation in the genus suggest massive reticulation in the past, involving both diploid and polyploid species with not yet stabilized asexual reproduction and polyploid apomicts with rare residual sexuality. Recurrent polyploidization was accompanied by multiple shifts to apomixis, which allowed the survival of selected polyploid lineages (Fehrer *et al.*, 2009; Krak *et al.*, 2013; Mráz *et al.*, 2019; Chrtek *et al.*, 2020). As a result of these processes, the vast majority of *Hieracium* apomicts are allopolyploids, while autopolyploids appear to be extremely rare, as suggested for *H. alpinum* (Mráz *et al.*, 2009). In the past, reticulation events often occurred in secondary contact zones, as many taxa involved in these hybridization events are currently allopatric (Fehrer *et al.*, 2009). The geographic distribution of “frozen” combinations of ancestral parental genomes in obligate or nearly obligate apomicts provides an excellent tool for tracing past biogeographic processes (Mráz *et al.*, 2019).

The young origin of the genus, dated to ~3.1 Mya, rapid diversification with shared ancestral polymorphism and incomplete lineage sorting, massive reticulation and frequent extinctions are the main factors that have deeply shaped the phylogenetic patterns in the genus (Fehrer *et al.*, 2009; Krak *et al.*, 2013; Fehrer *et al.*, 2022). Of the molecular markers used so far, i.e. nuclear ITS, ETS, two low-copy nuclear genes and two cpDNA loci, only ETS provided the best approximation

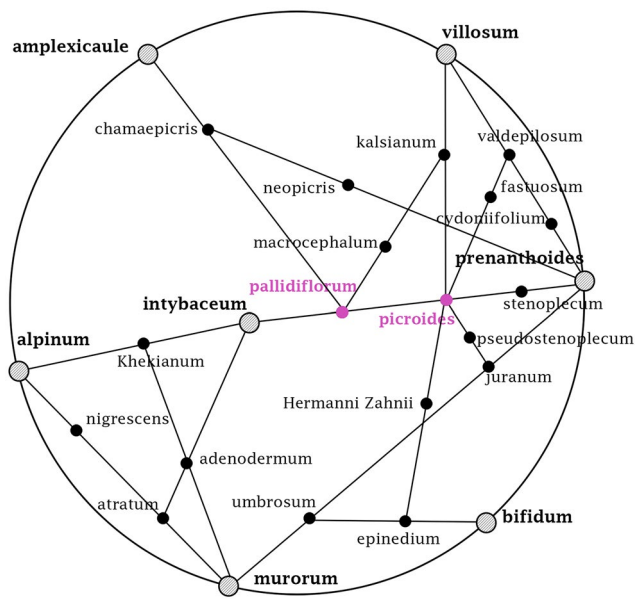


for resolving species relationships (Fehrer *et al.*, 2009; Krak *et al.*, 2013). The ETS-based tree suggests two supported groups, a slightly older “eastern” group including diploids from the Carpathians, Balkans and the eastern Alps and widespread *H. umbellatum*, and the “western” group including diploid taxa from western Europe (Fehrer *et al.*, 2009; Mráz *et al.*, 2019; Fehrer *et al.*, 2022; Figure 4). This differentiation correlates with haploid genome size being significantly higher in taxa from the eastern clade (Chrtek *et al.*, 2009). The use of remaining markers often results in polytomies, but these markers, especially low-copy nuclear genes,

have allowed the detection of parental alleles and the identification of multiple origins of allopolyploid apomicts (Mráz *et al.*, 2019; Chrtek *et al.*, 2020). Population genetic approaches (allozymes, RAPDs, AFLPs) revealed the presence of one or a few unique multilocus genotypes for particular apomictic microspecies thus supporting their recognition (e.g. Shi *et al.*, 1996; Mráz *et al.*, 2001; Štorchová *et al.*, 2002; Chrtek *et al.*, 2007; Ronikier and Szelağ, 2008). Substantially higher genetic variation suggesting polytopic origin was found in widespread triploid *H. alpinum* (Shi *et al.*, 1996; Štorchová *et al.*, 2002).



**Figure 4.** Phylogenetic Bayesian tree based on the most complete sampling of diploid species of *Hieracium* s.str. and the cloned ETS region (after Mráz *et al.*, 2019, updated). Diploid taxa are grouped into two main clades, the Western and the Eastern, according to the geographic distribution of diploids. Two triploid apomictic species were also included: ‘*H. racemosum* (3x)’ (in green), whose ETS alleles clustered with the diploid *H. racemosum*, and the allotriploid ‘*H. telekianum* (3x)’ (in black bold) which shows three divergent alleles, each related to one of three different parental diploid species: *H. vranceae*, *H. pojoritense*, and *H. sparsum*. For more details see Mráz *et al.*, (2019) (copyright with the authors).



**Figure 5.** Morphological relationships of basic (hatched larger circles, species epithets in bold larger letters) and intermediate species (solid smaller circles, species epithets in normal smaller letters) showing morphological affinity to a basic species *Hieracium intybaceum* (in the center) as proposed by Zahn (redrawn from Zahn 1921: 744, Figure 54). This scheme (a hypothesis) illustrates putative origins of intermediate species based on sharing of basic species' phenotypes. The position of two intermediate allotriploid species (both in magenta) – *H. pallidiflorum* morphologically closer to the basic *H. intybaceum*, and conversely, *H. picroides* closer to the basic *H. prenanthoides* – was confirmed by morphometric, molecular and cytogenetic analyses; the latter approach revealed two *intybaceum* and one *prenanthoides* subgenomes in *H. pallidiflorum*, and the reverse pattern, i.e. two *prenanthoides* subgenomes and only one *intybaceum* subgenome in *H. picroides* (Chrtek *et al.*, 2020).

The reticulate pattern of morphological variation in both *Hieracium* and *Pilosella* was already recognized by Nägeli (1866), who proposed a system of basic and intermediate species. The former species have a unique morphology, while the latter combine morphological characteristics of two or more basic species and are thought to be the result of hybridization between basic species (Zahn, 1921–1923; Figure 5). This system thus provides an excellent research framework for testing hybridogeneous origins and for the quantitative assessment of the genomic contribution of putative parental taxa. Using an integrative approach that included ploidy level and reproductive mode analyses, multivariate morphometrics, multiple molecular markers, and cytogenetics (Genomic in-situ hybridization and Fluorescence in-situ hybridization), Chrtek *et al.*, (2020) demonstrated the multiclonal character of two allotriploid species – *H. pallidiflorum* and *H. picroides*, for which the morphological

differentiation clearly corresponds to the inverse genome dosage of both parental taxa involved in the origin of both allotriploid apomicts, thus confirming the pattern already suggested by Zahn (Zahn, 1921–1923; Figure 5).

Taxonomic treatments of *Hieracium* vary between different European authors. The so-called Central European school of “hieraciology” accepts broadly defined species divided into subspecies, varieties, etc. (Zahn, 1921–1923; recently, e.g. Greuter, 2007; Greuter and Raab-Straube, 2008), while the Scandinavian, British, and Russian schools, including some other botanists, use a narrower species concept and treat all morphologically recognizable and constant forms at species rank (recently, e.g. Szelağ, 2003; Chrtek *et al.*, 2007; Tennant and Rich, 2008; Tyler and Jönsson, 2013; Tyler, 2017). Schuhwerk (2002) suggested treating fixed, morphologically distinct taxa, exceeding the framework of broad species as (micro) species, while treating as subspecies those with morphologically minor deviations with similar chorological and/or ecological behavior.

Here, firstly, we propose to adopt a broader taxonomic concept for sexual diploid taxa due to the greater and continuous variation caused and maintained by ongoing gene flow (Mráz *et al.*, 2019). Second, apomictic allopolyploids derived from different or the same parental combinations, which are morphologically and genetically well differentiated entities, should be recognized at the species level. By contrast, entities that differ from each other only by a few and usually minute characters and that are likely to have arisen from the same or related hybrid combinations or by autopolyploidization of diploid lineages showing more or less continuous variation, should be merged into more broadly defined species.

## 2. *Pilosella*

*Pilosella* is native to Eurasia and northwestern Africa and has been introduced and often naturalized in the Americas, Australia and New Zealand (Zahn, 1921–1923; Chapman *et al.*, 2000; Williams and Holland, 2007). The number of recognized species depends on the adopted concept. Recently, 122 “collective” (basic and intermediate together) species have been recognized in the genus (Bräutigam and Greuter, 2007).

Although closely related to *Hieracium*, *Pilosella* differs greatly in the type and frequency of apomixis. Whereas in *Hieracium* we can mostly see apomictically “frozen” results of past evolutionary processes, in *Pilosella* we can see evolution happening right in front of our eyes. This is because *Pilosella* has a significantly higher incidence of facultative sexuality than

*Hieracium*. In addition to frequent homo- and heteroploid hybridization, the extensive morphological and genetic variation in *Pilosella* is also caused by the co-occurrence of sexual and apomictic types with considerable variation of cytotypes, and frequent vegetative clonal growth, which also plays a crucial role in the establishment and evolution of new cytotypes (Krahulcová *et al.*, 2000; Šingliarová *et al.*, 2023).

In natural populations, *Pilosella* occurs at seven different ploidy levels, ranging from diploid ( $2n=18$ ) to octoploid level ( $2n=72$ ), and the majority of species are represented by more than one ploidy level with the highest cytotypic variation (five ploidies) recorded in *P. echioides* (Trávníček *et al.*, 2011) and the autopolyploid *P. rhodopea* (Šingliarová *et al.*, 2019). Diploids are sexual and strictly self-incompatible, but autogamy can be induced by a mixture of heterospecific pollen via mentor effects (Krahulcová *et al.*, 1999). The relationship between ploidy and mode of reproduction in polyploids is much more complex than in *Hieracium* and varies between among. Polyploids can be sexual (up to the hexaploid level) or apomictic with varying degrees of residual sexuality (up to 10% of the resulting progeny; Krahulcová *et al.*, 2000; 2014). Recent hybrids are either sterile or have a variable breeding system with high levels of residual sexuality and, consequently, extremely variable progeny. This can include polyhaploids resulting from a parthenogenetic development of reduced female gametes, often nonviable or sterile, which occasionally duplicate their genome, thus completing the polyploid-polyhaploid-polyploid cycle (Krahulec *et al.*, 2011).

Homo- and heteroploid hybridization is very common in *Pilosella*, and both basic and intermediate (hybridogeneous) species as well as recent hybrids can participate as parents. Such hybridization can involve both sexuals and (facultative) apomicts, and the latter can act as both pollen donor and seed parent (Gadella, 1987; Krahulcová *et al.* 2000; Fehrer *et al.* 2007b). Consequently, such hybridization events often result in a huge diversity of progeny. For instance, experimental crosses between facultatively apomictic hexaploid *P. rubra* (an intermediate hybridogeneous species between *P. aurantiaca* and *P. officinarum*) and sexual tetraploid *P. officinarum* resulted in three progeny classes: apomictic (hexaploid progeny, ca. 88%), haploid parthenogenetic (triploid progeny, ca. 4%) and hybrid (*P. aurantiaca* × *officinarum*, ca. 8%), which included pentaploids ( $3n+2n$  reduced gametes), heptaploids ( $3n$  reduced +  $4n$  unreduced gametes), and octoploids ( $6n$  unreduced +  $2n$  reduced gametes) (Krahulcová *et al.* 2004; Krahulec *et al.* 2006). Similar

diversity has been observed in open-pollinated plants of the same species under field conditions (Doležal *et al.* 2020).

In contrast to the genus *Hieracium*, apomixis in *Pilosella* is expressed as apospory of the *Hieracium*-type (unreduced 8-nucleate embryo sac anatomically similar to the *Polygonum*-type) and is often facultative (Rosenberg, 1906). Facultative apomixis has been demonstrated cytoembryologically in several species, such as the polyploid complex of *P. aurantiaca* (studies by A. Skalińska, reviewed in Krahulcová *et al.*, 2000; Koltunow *et al.*, 1998), *P. officinarum* (Turesson, 1972; Pogan and Wcisło, 1995), *P. caespitosa* (Skalińska and Kubień, 1972), and more recently in 16 species, natural and experimental hybrids (Hand *et al.*, 2015). Male meiosis appears to be regular in some tetraploid apomicts (Christoff, 1942). Even in apomicts with an odd number of chromosome sets, microsporogenesis is less disturbed than megasporogenesis (e.g. *P. officinarum*, Pogan and Wcisło, 1995). Pentaploids can thus serve as pollen donors (e.g. in *P. officinarum*, Gadella, 1987; 1991; 1992). Pollen analyses revealed no significant differences in pollen staining between sexuals, apomicts and female-sterile or semi-sterile plants. In contrast, the effects of both ploidy level and plant origin were significant (Rotreklová, 2004; Rotreklová and Krahulcová, 2016).

*Pilosella* has become an important model to disentangle the genetic basis of apomixis. Two dominant independent loci have been identified: the LOA (*LOSS OF APOMEIOSIS*) locus is required for apomeiosis (apospory) and suppression of the sexual pathway, while the LOP (*LOSS OF PARTHENOGENESIS*) enables autonomous embryo development (Catanach *et al.*, 2006; Koltunow *et al.*, 2011; Hand and Koltunow, 2014). A third locus controlling autonomous endosperm formation (AutE) has also been identified (Hand *et al.*, 2015; Bicknell *et al.*, 2016).

Phylogenetic relationships in *Pilosella* have been little studied. Of the molecular markers used, i.e. the nuclear ITS and two cpDNA loci, only ITS results are consistent with morphology and other evidence and are therefore considered to reflect the true phylogenetic relationships among the basic *Pilosella* species (Fehrer *et al.*, 2007a). In contrast, variation in the plastid markers divided *Pilosella* into two haplotype groups, named *Pilosella* I and II, with partially distinct but highly overlapping geographic ranges (the former having a more westerly distribution in Europe compared to the latter) (Fehrer *et al.*, 2007a). This analysis nested separately each of the closely related Mediterranean genera *Hispidella* and *Andryala* within the *Pilosella* I and the *Pilosella* II groups, respectively.

Chloroplast capture events were proposed as the most likely explanation for these incongruencies between plastid and nuclear DNA markers (Fehrer *et al.*, 2007a).

As a consequence of the ongoing gene flow across ploidies and reproductive modes, and thus a wider and more continuous morphological and genetic variation, the recently proposed infrageneric classification and species concept in *Pilosella* are broader than in *Hieracium* (Bräutigam and Greuter, 2007). This classification includes (i) more or less broadly defined basic species and aggregates (with species and subspecies), and (ii) intermediate (hybridogeneous), so-called “collective” species. The latter are of very variable nature and value: they may include only newly formed primary hybrids or correspond to stable hybridogenous species occurring independently of their parents. They often include both types, usually occurring in different regions (Bräutigam and Greuter, 2007). Other concepts were summarized and discussed in detail in Schuhwerk (2002) and Majesky *et al.*, (2017).

## V. Conclusions and outlook

Our survey reveals that much more work is still needed before we can have a defined view of the role apomixis plays -if any- on macroevolution and in shaping the angiosperm phylogeny. Reliable assessments of occurrences of apomixis in angiosperms like that of Hojsgaard *et al.*, (2014b), Hojsgaard and Pullaiah (2023) or Hörandl (2024), including reexamination of doubtful cases, will certainly provide an unbiased outlook of the consequences of apomixis in plants. The great diversity of developmental pathways, with multiple origins of various modes of apomixis in angiosperms, is a major problem for delineating one singular scheme for the evolution of apomixis. Our review further emphasizes that apomixis cannot be seen in isolation from embryological features, breeding systems (self-compatibility vs. self-incompatibility), and from cytology and ploidy levels. Cytogenetic analyses are promising for understanding origins of apomixis, as exemplified in *Boechera* and *Hieracium*. Future efforts should also include assessments on species from the many families and genera of angiosperms that have not been studied so far.

Major progress in phylogenetic/phylogenomic analyses and also experimental work established that apomixis frequently arises from hybridization, in connection with polyploidy or on the diploid level (as in exemplified in *Boechera*); see reviews in Hojsgaard and Hörandl (2019) and Hojsgaard and

Pullaiah (2023). Beside the assessment of reticulate relationships, the widely used FCSS method allows for a large-scale quantification of facultative apomixis, and for detection of ploidy shifts in the offspring (e.g. Mráz and Zdvořák, 2019). Furthermore, environmental influence on mode of reproduction and biogeographical trends can be screened efficiently. The method thus has the potential to give insights into the short-term evolutionary dynamics of apomixis. However, accurate interpretation of FCSS patterns should be based on a solid knowledge of embryo sac formation in a studied taxon (typically genus), ploidy level of plants and further biological traits. Understanding the mechanisms of origins of apomixis in natural populations, combined with genomic analyses, will also improve our insights into the genetic basis of apomixis. So far, our survey suggests multiple pathways to apomixis, including also environmental influence, which would infer diverse and complex genetic and epigenetic control mechanisms. Still, the long-term fate of apomictic lineages is unclear. Theoretically an apomictic complex could persist for quite some time via residual sexuality and clonal turnover. Empirically it is still unclear how long in evolutionary time apomictic lineages may exist in plants before mutational decay would drive them to extinction (Hodač *et al.*, 2019; Hörandl, 2024). Despite their reduced genetic variation when compared to related sexuals, apomictic lineages could increase their evolutionary potential through environmentally-triggered adaptive and heritable epimutations (Verhoeven and Preite, 2014) as has been shown in plants reproducing by vegetative growth (e.g. Rendina González *et al.*, 2016). However, more empirical evidence about this process in apomictic plants is much needed. Furthermore, it is still not well documented with phylogenetic analyses whether permanent reversals from apomictic lineages to obligate sexual lineages are possible (e.g. Chapman *et al.*, 2000). Cytoembryological or FCSS analysis alone gives just a “snapshot” of the versatile modes of reproduction that may exist in parallel in an evolutionary lineage, which makes it impossible to assess ancestral states. For these questions, whole-genome analyses and phylogenomics, also for wild plants, are most wanted to understand better the long-term genome evolution and functionality of apomictic plants.

The great diversity of apomictic pathways mentioned above, and the broad taxonomic distribution, further hampers the applications of taxonomic concepts, especially on the species level. The fact that apomixis has emerged independently in evolutionarily divergent genome lineages that show different



responses in terms of genomic dosage, developmental flexibility, and ecological plasticity, also prevent a unified use of a single species concept for all apomicts. Many phenotypically described agamospecies do not fulfill the criterion of species being an evolutionary lineage, and case-by-case decisions are needed (Hörandl, 2022). For evolutionary species concepts, the many evolutionary pathways result necessarily in a pluralism of concepts and taxonomic treatments, as summarized here. Understanding better short- and long-term evolution of apomictic lineages is crucial for well-founded taxonomic treatments.

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